
# Microsaccades as a Window to Visuospatial Attention: Evidence by the Simultaneous Recording of Eye Movements and EEG

**D i s s e r t a t i o n**

**zur Erlangung des akademischen Grades doctor rerum naturalium (Dr. rer. nat.)**

**im Fach Psychologie**

eingereicht an der Lebenswissenschaftlichen Fakultät
Humboldt-Universität zu Berlin

von Dipl.-Psych. Susann Meyberg

Präsidentin der Humboldt-Universität zu Berlin: Prof. Dr.-Ing. Dr. Sabine Kunst
Dekan der Lebenswissenschaftlichen Fakultät: Prof. Dr. Bernhard Grimm

Gutachter
1. Prof. Dr. Werner Sommer
2. Prof. Dr. Ralf Engbert
3. Dr. Martin Rolfs

Tag der Verteidigung: 5. April 2017

# Table of contents


Danksagung ..... 1

List of original articles ..... 3

Abstract ..... 5

Zusammenfassung ..... 7

Synopsis of the thesis ..... 9

1 Introduction ..... 9

2 Theoretical and empirical background ..... 13

2.1 Visual attention ..... 13

2.2 Microsaccades and visual attention ..... 19

2.3 ERP correlates of visual attention and microsaccades ..... 22

3 Summary of results ..... 29

3.1 Overview of the thesis ..... 29

3.2 Study 1: Microsaccades and the selection of visual stimuli ..... 31

3.3 Study 2: Microsaccades and lateralized cue-ERPs ..... 34

3.4 Study 3: Microsaccade-related potentials and covert attention ..... 35

4 Discussion and integration of results ..... 39

4.1 Microsaccades and visual attention ..... 40

4.2 Microsaccades: Challenges and perspectives in EEG research ..... 64

4.3 Conclusion ..... 71

References ..... 73

# Mein Dank gilt …

… Werner Sommer für die Betreuung meiner Dissertation und Unterstützung in den letzten Jahren. Werner, Du hast bereits im Grundstudium meine Leidenschaft für die Biologische Psychologie geweckt und mir im Rahmen meiner Dissertation die Freiheit geben, meinen Forschungsinteressen nachzugehen. Nichtsdestotrotz standest Du mit Deinem geballten Wissen jederzeit zur Verfügung – das habe ich nie für selbstverständlich erachtet.

… Olaf Dimigen für seine Expertise zur Koregistrierung von EEG und Blickbewegung, die er stets gerne geteilt hat. Olaf, Du hast mich nicht nur für das Thema Mikrosakkaden begeistert, sondern von Dir habe ich gelernt, dass die Untersuchung kleiner Augenbewegungen sehr viel Hingabe zum Detail erfordert. Dein Beitrag war für die Anfertigung dieser Arbeit von unschätzbarem Wert.

… Petra Sinn für viele Dinge, die weit über unsere Zusammenarbeit hinausgehen. Petra, hier danke ich Dir im Besonderen dafür, dass Du mir einen Einblick in die aufregende Welt der komputationalen Modellierung gegeben hast.

… Markus Werkle-Bergner für seine thematische Offenheit und seine unterstützende und positive Art im Umgang mit Problemen.

… Ralf Engbert für spannende Diskussionen zu Mikrosakkaden. Ihm und Martin Rolfs gebührt zudem mein herzlicher Dank für die Begutachtung meiner Dissertation.

… Thomas Pinkpank und Rainer Kniesche für Ihre ständige Ansprechbarkeit bezüglich aller technischen Fragen rund um das Labor.

… Ulrike Bunzenthal, Linda Gerresheim, Nicola Hohensee, Niels Krause, Kerry Moore, Andrea Paulenz und Lisa Spiering für Ihre Unterstützung bei der Rekrutierung von Probanden und den Datenerhebungen. Danke, dass Ihr mir die Arbeit wesentlich erleichtert habt.

… meiner Familie und meinen Freunden. In den letzten Jahren ward Ihr es, mit denen ich Freude und Leid in allen Lebenslange teilen durfte. Das habe ich stets als ein Privileg empfunden. Für Euch werde ich jetzt wieder mehr Zeit haben!

# List of original articles

1. Meyberg, S., Sinn, P., Engbert, R., and Sommer, W. (2017). Revising the link between microsaccades and the spatial cueing of voluntary attention. *Vision Research, 133(2017),* 47-60.

2. Meyberg, S., Sommer, W., and Dimigen, O. (2017). How microsaccades relate to lateralized ERP components of spatial attention: A co-registration study. *Neuropsychologia, 99(2017),* 64-80.

3. Meyberg, S., Werkle-Bergner, M., Sommer, W., and Dimigen, O. (2015). Microsaccade-related brain potentials signal the focus of visuospatial attention. *Neuroimage, 104*(0), 79-88.

# Abstract

It is well-known that visual attention and saccades are tightly coupled under normal viewing conditions. Nonetheless, most studies of visual attention implement processes of covert attention; that is, when attention is directed during fixation periods in the absence of larger saccades. While previous EEG studies have provided tremendous insight into the neural network that controls the deployment of covert attention, these studies fail to account for the inevitable occurrence of fixational saccades. In contrast, previous eye tracking (ET) studies have established reliable links between these so-called microsaccades and covert attention, but have not directly related their findings to seminal EEG results. This thesis aims to bridge the gap between previous EEG and ET studies by investigating the link between well-established event-related potentials (ERPs) of endogenous attention and microsaccades. To this end, three studies were conducted with concomitant ERP and high-resolution ET recordings. In these studies, participants performed a Posner spatial cueing task in which an endogenous cue indicated the location of a peripheral target stimulus.

As the key finding of this thesis, we show that microsaccades relate to neural correlates of visual attention. First, microsaccades and an early posterior ERP reflected the top-down selection of a visual stimulus based on its features: Both variables were mainly aligned with the relevant cue stimulus but not with the covert attention shift initiated by that cue. Although this result challenges previous ET studies that reported a close link between microsaccades and cued attention shifts,

it is consistent with the concept of a neural network that selects relevant stimuli from distracting ones and directs behavior toward selected stimuli. Second, microsaccadic gaze shifts evoked a visual potential in the EEG that was enhanced for stimuli in the focus of attention; a finding that is well-established for the visual potential measured after the presentation of a stimulus. Importantly, these microsaccade-related potentials provided a fine-grained temporal index of the subject's attentional state. Finally, microsaccades further evoked a corneoretinal artifact overlooked in previous EEG studies. This artifact contaminated the measurement of a frontal ERP previously associated with preparatory attentional control. In sum, this thesis supports the idea that covert attention is accompanied by significant oculomotor activity and provides first evidence for the benefits of using concomitant ERP and ET recordings to explore the link between microsaccades and visual attention.

# Zusammenfassung

Visuelle Aufmerksamkeit und Sakkaden hängen eng zusammen, wenn der Blick frei ausgerichtet werden darf. Experimente zu visueller Aufmerksamkeit basieren jedoch oft auf verdeckten Aufmerksamkeitsprozessen; das heißt, wenn der Aufmerksamkeitsfokus trotz strikter Fixation verschoben wird ohne dabei eine größere Sakkade auszuführen. In Studien mit Elektroenzephalogramm (EEG) konnte das neuronale Netzwerk identifiziert werden, dass verdeckte Aufmerksamkeitswechsel steuert. Diese Studien ignorieren jedoch oftmals das unvermeidbare Auftreten von Fixationssakkaden. Studien mit Eye-Tracking (ET) hingegen belegen einen Zusammenhang zwischen Aufmerksamkeit und diesen sogenannten Mikrosakkaden, beziehen ihre Ergebnisse jedoch nicht direkt auf etablierte EEG-Befunde. Das Ziel dieser Dissertation ist, bestehende EEG- und ET-Befunde aufeinander zu beziehen, indem der Zusammenhang zwischen ereigniskorrelierten Potentialen (ERP) endogener Aufmerksamkeit und Mikrosakkaden untersucht wird. Folglich wurden drei Studien mit gleichzeitiger Erfassung von EEG und hochauflösendem ET durchgeführt. In den Studien haben die Probanden ein ‚Posner Spatial-Cueing-Paradigma' absolviert, in dem ein endogener räumlicher Hinweisreiz die Position eines peripheren Zielreizes anzeigte.

Als Kernbefund dieser Dissertation zeigte sich, dass Mikrosakkaden mit neuronalen Korrelaten visueller Aufmerksamkeit zusammenhängen. Erstens, Mikrosakkaden als auch eine frühes posteriores ERP reflektierten die Selektion von visuellen

Reizen basierend auf deren Merkmalen: Beide Variablen zeigten überwiegend eine räumliche Selektivität für den aufgaben-relevanten Hinweisreiz, aber nicht für den Aufmerksamkeitswechsel, der durch den Hinweisreiz ausgelöst wurde. Dieses Ergebnis widerspricht früheren ET-Befunden eines starken Zusammenhangs zwischen Mikrosakkaden und instruierten Aufmerksamkeitswechseln, lässt sich jedoch vereinbaren mit dem Konzept eines Netzwerkes, dass relevante Reize unter Distraktoren selektiert und Bewegungen hin zu selektierten Reizen initiiert. Zweitens, Blickbewegungen durch Mikrosakkaden erzeugten ein visuelles Potential, das verstärkte Potentialkomponenten für Reize zeigte, die im Aufmerksamkeitsfokus lagen. Ein ähnlicher Befund ist gut etabliert für das visuelle Potential, das üblicherweise nach der Präsentation eines Reizes gemessen wird. Weiterhin zeigte sich, dass das Mikrosakkaden-evozierten Potential einen zeitlich gut aufgelösten Index des Aufmerksamkeitsfokus darstellt. Drittens, Mikrosakkaden erzeugten zudem ein korneoretinales Artefakt, dass in früheren Studien übersehen wurde. Dieses Artefakt kontaminierte die Messung eines frontalen ERPs, dass zuvor mit der Kontrolle von Aufmerksamkeitsprozessen in Zusammenhang gebracht wurde. Zusammenfassend bestätigt diese Dissertation die Annahme, dass verdeckte Aufmerksamkeit von signifikanter okulomotorischer Aktivität begleitet wird und dass die gleichzeitige Erfassung von EEG und Blickbewegungen bedeutsame Einblicke in den Zusammenhang von Mikrosakkaden und visueller Aufmerksamkeit erlaubt.

# Synopsis of the thesis

## 1 Introduction

Our environment provides more information than can be processed in a single moment. Imagine looking for your friend in an overcrowded train station. Today is the final match of the football championship, and many people, like you, are on their way to the stadium. You are already late to meet your friend and most of the sport fans around you rush through the station hall wearing the jersey of the favorite team. How are you going to find a single person in that seemingly uniform crowd of several hundred people? Luckily your friend just texted you that he is waiting at the east exit. However, when you reach the exit you are still faced with a group of people waiting there. At that moment, you remember that your friend has a very special sense of humor and will probably be wearing the jersey of the underdogs and he may even be wearing that silly hat he bought … Ah, there he is …

The mechanism of prioritizing relevant information in cluttered environments is called attention and is crucially based on the location and the features of sensory information. In fact, in everyday situations, there are many internal and external cues that instruct *where* to look for something (i.e., location-based attention), for example, close to the east exit, and *what* to look for (i.e., feature-based attention), for example, the color of your friend's jersey. These cues can be used to bias the perceptual processing of incoming information. In addition, attention does not only improve perception, but also involves goal-directed behavior, for example, walking

toward the exit or sequentially looking at each person of a group to find your friend (Allport, 1987).

In attention research, however, experimental tasks often require strict movement control. In the commonly used Posner spatial cueing task, a cue stimulus informs the participant where to expect an upcoming target stimulus. Attention then has to be shifted toward the to-be-attended target location while fixation is maintained; a process called 'covert attention' as it occurs in the absence of larger saccades (Posner, 1980). What has been neglected in studies on the spatial cueing of covert attention is that eyes are never motionless, but move even during fixation. Among these fixational eye movements, microsaccades (MSs) have been shown to align with the focus of covert attention (e.g., Engbert & Kliegl, 2003; Hafed & Clark, 2002). Thus, instead of assuming that (covert) attention can be studied in the absence of significant oculomotor activity (Posner, 1980; Carrasco, 2011), in this thesis we hypothesized that MSs are part of the neural network that controls the deployment of attention. To investigate this claim, we conducted three spatial cueing studies and combined the recording of eye movements and event-related potentials (ERPs) of attention.

The main goal of this thesis was to investigate the correlation of MS dynamics with location- and feature-based attention, as well as with the ERP correlates of both attentional mechanisms. Neuroimaging and electrophysiological studies have revealed that these mechanisms are mediated by a cortical network of frontoparietal areas (e.g., Corbetta & Shulman, 2002) and subcortical areas such as the superior colliculus (e.g., Krauzlis, Lovejoy, & Zenon, 2013). Since these brain areas not only

play a crucial role in attention, but also greatly overlap with the neural network controlling overt attention which involves the execution of saccades (e.g., Corbetta, 1998), we expected the following: First, during spatial cueing of attention, MSs may not exclusively align with the location-based selection of the to-be-attended target location as shown previously (e.g., Engbert & Kliegl, 2003), but also with the selection of the cue stimulus based on its visual features. In fact, such an additional feature-based selection mechanism is often present, albeit neglected in spatial cueing tasks (e.g., Van Velzen & Eimer, 2003). Thus, in Study 1 and 2, we systematically related MS dynamics to location- and feature-based attention in a spatial cueing task by using an experimental design that allows dissociation of both attentional mechanisms. Second, we speculated that MSs might correlate with attention-related ERPs that reflect the involvement of the frontoparietal network with attention (e.g., Corbetta & Shulman, 2002). More specifically, in Study 2, we related MSs to ERPs of preparatory attentional control (e.g., Harter, Miller, Price, Lalonde, & Keyes, 1989). In Study 3, we investigated ERP effects that reflect the modulation of sensory processing guided by top-down needs. The noteworthy point of this latter study was that these attention-related ERPs were observed after microsaccadic gaze shifts as compared with the traditional experimental approach of investigating ERPs that emerge after the presentation of a stimulus (e.g., Eimer, 2014).

As a further goal of this thesis we assessed if ERPs of visual attention are prone to artifacts (Study 2 and Study 3). These artifacts may be caused by the temporal overlap of ERPs elicited by the presentation of a stimulus, for example, a cue

stimulus that directs attention, and ERPs elicited by the execution of a MS. Most importantly, in Study 2, we tested if ERPs of preparatory attentional control are contaminated by the corneoretinal artifact introduced by microsaccadic shifts of the gaze.

In chapter 2, I will review the theoretical frameworks and previous findings about location- and feature-based mechanisms of attention, as well as the relation between visual attention and MSs. Then, the neural correlates of visual attention will be introduced focusing on their potential link to MSs. Chapter 3 will give an overview of the research objectives of the conducted studies in this thesis and a detailed description of the main results of each study. Finally, in chapter 4, I will relate the results of this thesis to the previous research in this area and provide possible future research questions. Chapter 4 ends with concluding remarks.

# 2 Theoretical and empirical background

## 2.1 Visual attention

### 2.1.1 Location-based vs. feature-based attentional selection

Attention refers to a mechanism that selects sensory information of relevance for subsequent behavior while ignoring irrelevant information – a selection probably dictated by limited cognitive and neural resources for storing and processing information in crowded environments (Broadbent, 1954; Desimone & Duncan, 1995; Treisman, 1964). In the visual domain, two general mechanisms for achieving selectivity are distinguished:

With *location-based selection,* stimuli are favored that are presented within the focus of attention (i.e., the 'spotlight of attention') regardless of their visual attributes (Eriksen & James, 1986; Posner, 1980). Location-based selection is commonly investigated in the Posner spatial cueing task, in which a cue stimulus provides information about the location of an upcoming target stimulus (experimental procedure is detailed below). With prior spatial information, perceptual judgments about the target are facilitated and more accurate (Posner, 1980; Posner & Cohen, 1984); a finding that has been linked to enhanced neural representations for attended targets when compared to unattended targets (Eimer, 1993; Hillyard, Vogel, & Luck, 1998; Van Voorhis & Hillyard, 1977).

In contrast, with *feature-based selection,* stimuli are favored with respect to their inherent features, for example, color, orientation, or direction of motion, without

prior information about their location. This mechanism is traditionally investigated with the visual search task, in which the presence or absence of a pre-defined target in a crowded stimulus array is reported. A general finding is that search is fast and efficient when targets can be distinguished from distracting items based on a unique feature, while search is less efficient if a target is defined by a combination of features (Treisman & Gelade, 1980). It has been suggested that presenting a target along with distractors leads to competition between stimuli for neural and cognitive representation. This 'biased competition' is thought to take place at different levels of visual processing and attentional selection therefore reflects the integration of the bottom-up saliency of the stimuli as well as the top-down intentions related to the task (Beck & Kastner, 2009; Desimone & Duncan, 1995).

### 2.1.2 Spatial cueing of covert attention

Studies investigating location-based attention commonly implement processes of *covert attention,* for example, in spatial cueing tasks. During covert attention, the focus of attention is directed without eye movements. In contrast, *overt attention* can involve a movement of the head or gaze toward a relevant object (e.g., Posner, 1980). In the Posner spatial cueing task, participants are asked to maintain fixation, but to covertly attend to a peripheral target location indicated by a cue stimulus (e.g., a central arrow cue pointing toward the left hemifield). The participant then has to detect, localize, or identify the target stimulus. To probe for the person's attentional focus, the validity with which the spatial cue predicts the target location is manipulated: The target appears at the to-be-attended location in valid-cue trials, and at a not-to-be-attended location in invalid-cue trials. In neutral trials, no

information about the target location is provided (Posner, 1980; see also Carrasco, 2011).

It is a well-known that attention can be oriented *exogenously,* in a stimulus-driven manner and *endogenously,* in a goal-driven manner controlled by top-down needs (Jonides, 1981). Both mechanisms exhibit very distinct dynamics (e.g., Müller & Rabbitt, 1989; e.g., reviewed in Egeth & Yantis, 1997; Kinchla, 1992). An exogenous cue, for example, an abruptly-appearing peripheral flash, captures attention within 100-200 ms (e.g., Müller & Humphreys, 1991). In contrast, after an endogenous cue, for example, a central arrow cue, it takes about 300 ms to deploy endogenous attention. The attentional focus can then be held at the to-be-attended location even for extended periods of time (Posner, 1980; Sarter, Givens, & Bruno, 2001). In the present thesis, three spatial cueing studies using central arrow cues will be presented.

### 2.1.3 Spatial cueing as an implementation of purely covert orienting?

The assumption that activity measured in spatial cueing tasks can solely be attributed to the deployment of covert attention is challenged by at least two phenomena: the occurrence of involuntary MSs and the necessity to process and select the spatial cue that directs attention.

***Attention and eye movements.*** It has been argued that an important function of visual attention is not only to enhance perception, but to control goal-directed movement (Allport, 1987; Neumann, 1987). For example, under normal viewing conditions, there are many potential saccade goals, but the gaze can be shifted only

toward one location at a given moment. This gaze shift brings relevant objects closer to the fovea, that is, the part of the retina of highest visual acuity. Thus, generating a saccade may require the attentional selection of the endpoint of the upcoming saccade. Consistent with this idea, visual sensitivity has been shown to increase at the saccade goal before the eye movement is executed (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995; Montagnini & Castet, 2007).

Given this tight link between attention and saccades, it is a controversial question whether covert orienting also involves the preparation and control of goal-directed movements (recently reviewed in Deubel, 2014). The 'pre-motor theory of attention' proposes that the same control mechanism is at work both in shifting attention and in determining motor behavior toward a location (Rizzolatti, Riggio, Dascola, & Umilta, 1987). In this theory, improved visual sensitivity for stimuli presented at a to-be-attended location is thought to result from generating a saccade toward that location. Thus, activity during spatial cueing of covert attention reflects the generation of an unexecuted saccade as the task requires strict visual fixation (Rizzolatti & Craighero, 1998; Rizzolatti et al., 1987; Rizzolatti, Riggio, & Sheliga, 1994).

While the pre-motor theory has been very influential as it generates several explicit hypotheses, a strict version of this theory has been rejected on several grounds (e.g., reviewed in Smith & Schenk, 2012). However, supporting the idea that spatial cueing is accompanied by rich oculomotor activity, recent eye tracking studies showed a correlation between involuntary fixational eye movements and covert

attention (e.g., Engbert & Kliegl, 2003). It has long been known that eyes are never still, but exhibit three movements at a miniature spatial scale even during fixation periods (Barlow, 1952; Ditchburn & Ginsborg, 1953; Ratliff & Riggs, 1950). These movements comprise a curvy drift motion that is superimposed by a fast-oscillating tremor. This drift is interrupted by rapid MSs 1 or 2 times per second. MSs are conjugated eye movements of an amplitude below 1° that share several characteristics with saccades (e.g., reviewed in Martinez-Conde, Macknik, Troncoso, & Hubel, 2009; Rolfs, 2009).

A key finding that has inspired the research in this thesis is that the orientation of MSs closely aligns with the focus of covert attention (e.g., Engbert & Kliegl, 2003; Hafed & Clark, 2002; Pastukhov & Braun, 2010). Recently, it has been proposed that these systematic biases in MSs toward and away from a stimulus may even account for the fluctuations in perceptual performance classically attributed to attention (Hafed, Chen, & Tian, 2015; Tian, Yoshida, & Hafed, 2016). This strong claim can be interpreted as the 'microsaccade version' of the pre-motor theory of attention. To shed a deeper light on the link between eye movements and attention, it is the major aim of this thesis to investigate the relation between MSs and covert attention.

***Feature-based selection in the Posner spatial cueing task.*** A crucial element of spatial cueing procedures is the spatial cue that indicates where attention should be directed. It has been argued that a 'lateralized' endogenous cue triggers two attentional selection mechanisms: the location-based selection of the to-be-attended target location and the feature-based selection of task-relevant parts of the cue

stimulus (Van Velzen & Eimer, 2003). In particular, there is no doubt that, for example, a left-pointing arrow cue can initiate a covert shift of attention toward the left hemifield. However, to encode the task-relevant information from the cue stimulus effectively, processing of certain stimulus parts might be prioritized, in particular, the tip of the arrow. In fact, feature-based attention not only occurs for distinct stimuli in crowded search arrays, but has also been shown for local elements and parts of a stimulus (Treisman & Gelade, 1980).

In this thesis, a cue stimulus is called lateralized if its stimulus parts can be distinguished by their visual features and each part conveys a different amount of information about the target location. Thus, feature-based visual selection is not only triggered by asymmetric arrow cues, but also by symmetric cue stimuli as long as only certain distinct stimulus parts are task-relevant. An example is an odd-colored ring among four symmetrically arranged peripheral rings (e.g., Hafed, Lovejoy, & Krauzlis, 2011). The important problem that arises with most lateralized cues is that the hemifield where relevant stimulus parts are presented is also the hemifield that needs to be attended. Thus, if a dependent variable of interest – such as an ERP or an eye movement – shows spatial selectivity for the to-be-attended hemifield, it is not necessarily the case that this selectivity arose from a link between this variable and the cued attention shift. Instead, it could be related to the feature-based selection of the lateralized cue. To better understand the basis of spatial selectivity that has been observed for ERP components and MSs in previous studies with (uncontrolled) lateralized cues, in Study 1 and 2 we used a

cue stimulus that made it possible to dissociate the hemifield to-be-attended from the hemifield where task-relevant aspects of the cue were presented.

## 2.2 Microsaccades and visual attention

### 2.2.1 Covert orienting and the orientation of microsaccades

Given the similarities between saccades and MSs (e.g., Zuber & Stark, 1965), the close relationship observed between saccades and spatial attention (e.g., Deubel & Schneider, 1996), and the inevitable occurrence of MSs during fixation (e.g., Ditchburn & Ginsborg, 1953), a link between MSs and covert attention seems compelling. In fact, such systematic links have been reported for the *orientation of microsaccades* after attention-directing cues (e.g., Engbert & Kliegl, 2003; Hafed & Clark, 2002) and those effects closely follow the temporal dynamics of endogenous and exogenous attention (Kinchla, 1992; Müller & Rabbitt, 1989; see also *2.1.2 Spatial cueing of covert attention*):

In one of the first studies, Engbert and Kliegl (2003) used an endogenous central arrow cue pointing left or right that instructed participants to deploy covert attention toward the left or right hemifield, respectively. After the cue, the rate of MSs was shortly inhibited and then rebounded in the interval between 200-500 ms. Importantly, during this 'rebound' interval, MSs were biased toward the to-be-attended target location as compared to the not-to-be-attended location. In later studies, this tendency of MSs to move with the focus of cover attention has been replicated with arrow cues (Hermens & Walker, 2010; Laubrock, Engbert, Rolfs, & Kliegl, 2007; Laubrock, Kliegl, Rolfs, & Engbert, 2010; Wieczorek, 2016) and

extended to the presentation of symbolic color cues (Engbert & Kliegl, 2003; but see Laubrock, Engbert, & Kliegl, 2005) and gaze cues (Yokoyama, Noguchi, & Kita, 2012). In addition, these cue-related biases in MS orientation have been shown to predict subsequent reaction time (RT). In particular, RT is facilitated if a 'rebound' MS moved toward the location of the upcoming target as compared to a trial with a MS moving away from that location (Laubrock et al., 2007; Laubrock et al., 2010; but see Horowitz et al., 2007a, b). In contrast, RT can be prolonged if MSs occur late in the cue-target interval (Kliegl, Rolfs, Laubrock, & Engbert, 2009; Pastukhov & Braun, 2010), which was also observed in other tasks (e.g., Betta & Turatto, 2006).

Likewise, MSs align with attention also after exogenous cues. Resembling the rapid dynamics of exogenous attention, this effect occurs within 100 ms post-cue (Chen, Ignashchenkova, Thier, & Hafed, 2015; Hafed & Clark, 2002; Laubrock et al., 2005; Rolfs, Engbert, & Kliegl, 2005; Tian et al., 2016) and can be followed by a movement bias away from that location (Galfano, Betta, & Turatto, 2004; Laubrock et al., 2005; Rolfs et al., 2005; Tian et al., 2016). While the early orientation bias has been linked to the phenomenon of 'attentional capture' (Jonides, 1981), it has been suggested that the latter effect reflects the phenomenon of 'inhibition of return' (Posner & Cohen, 1984).

Correlations of MS dynamics with covert attention have been attributed to the large overlap of the neural networks that control eye movements and attention (Corbetta, 1998). In studies using electrophysiology (Hafed, Lovejoy, & Krauzlis, 2013) and computational modelling (Engbert, 2012; Hafed, Goffart, & Krauzlis, 2009), a key

role in mediating these correlations has been ascribed to the superior colliculus (SC). The SC is a midbrain structure that not only plays a crucial role in the generation of saccadic eye movements (e.g., Hafed et al., 2009; Robinson, 1972; e.g., reviewed in Munoz & Everling, 2004; Hafed, 2011), but is also involved in visual attention (e.g., Fecteau, Bell, & Munoz, 2004; Kustov & Robinson, 1996; reviewed in Krauzlis, Lovejoy, & Zenon, 2013).

### 2.2.2 Open question: Microsaccades and feature-based attention

The notion of a tight coupling between MSs and attention is now well-established (e.g., reviewed in Engbert, 2006; Hafed et al., 2015; Kowler, 2011; Laubrock et al., 2010; Martinez-Conde, Macknik, & Hubel, 2004; Rolfs, 2009). However, in the study by Engbert and Kliegl (2003) an alternative explanation for the effects of spatial cueing of endogenous attention on MS orientation was also addressed: MSs may not align with the cued attention shift but rather with the foveally presented cue stimulus indicating that shift. To test this hypothesis, Engbert and Kliegl (2003) conducted a control experiment in which participants were asked to fixate on a central arrow stimulus and to report the offset of the arrow via button press. With this task, MSs did not align with lateralized parts of the cue, in particular, the tip of the arrow stimulus. Thus, it was concluded that orientation biases after endogenous cues do not comprise a mere oculomotor reflex.

A limitation of this control experiment by Engbert and Kliegl (2003) is that in a simple fixation task the directional information of the arrow stimulus is irrelevant for solving the task. However, in spatial cueing tasks, encoding the directional information of the cue stimulus is a prerequisite for the covert attention shift. As

we outlined above, encoding this information from lateralized cues, such as an arrow stimulus, is thought to trigger a top-down mechanism for selecting the task-relevant parts of the cue based on their visual features (Van Velzen & Eimer, 2003; see *2.1.3 Spatial cueing as an implementation of purely covert orienting?*). Thus, in Study 1 and 2 we investigated if MSs not only align with the direction of a cued attention shift, but in addition – or alternatively – with this feature-based selection of the cue stimulus indicating that shift. If this latter alignment exists, we aimed at re-evaluating the correlation of 'rebound' MSs with response times previously reported (e.g., Laubrock et al., 2010). Finally, we simulated MS dynamics in a recent computational model on MS generation (Engbert, 2012; Engbert, Mergenthaler, Sinn, & Pikovsky, 2011). In contrast to a previous simulation study that explained cue-related orientation biases only by a location-based selection mechanism (Engberg, 2012), in Study 1 we implemented an additional mechanism for the feature-based selection of the lateralized cue, based on the distinct activity pattern of the SC in visual search tasks (McPeek & Keller, 2004).

## 2.3 ERP correlates of visual attention and microsaccades

### 2.3.1 Neural network for endogenous attention

Converging evidence from electrophysiology and neuroimaging points to the involvement of a dorsal frontoparietal neural network in controlling the endogenous (top-down) selection of stimuli (e.g., reviewed in Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002; Posner & Petersen, 1990). This cortical network includes the intraparietal sulcus and the superior parietal lobule of the parietal cortex as well as areas of the frontal cortex along the precentral sulcus which likely

also covers the frontal eye fields. As these regions are activated in expectation of an upcoming event even after transient cue-related (visual) activity has decayed, it was suggested that their main function is to generate and maintain top-down signals representing the person´s internal goals (e.g., Corbetta et al., 2008). These signals modulate the activity in visual areas to enhance processing of desired stimulus features and locations in the visual field (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Hopfinger, Buonocore, & Mangun, 2000; Moore & Armstrong, 2003; Ruff et al., 2006; Shulman et al., 1999).

Importantly, this frontoparietal network for covert attention greatly overlaps with the neural network for overt attention which involves the generation and execution of larger saccadic eye movements (Corbetta, 1998; Corbetta et al., 2008). In light of this finding, this thesis aimed at investigating if MS dynamics during covert attention correlate with the activity of the frontoparietal network, in particular, with ERPs of preparatory attentional control and with ERPs of the top-down modulation of visual stimuli. These ERPs and their potential link to MSs are discussed in the following sections.

### 2.3.2 Lateralized cue-ERPs of preparatory visual attention

It has been proposed that the activity of the frontoparietal network is reflected in lateralized ERP components measurable in the EEG after the presentation of a cue that directs attention (e.g., Eimer, van Velzen, & Driver, 2002; Harter et al., 1989; Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000; Praamstra, Boutsen, & Humphreys, 2005; Yamaguchi, Tsuchiya, & Kobayashi, 1994; reviewed in Eimer, 2014). In previous EEG studies, three cue-ERP components have been

reliably observed and are defined as the potential difference at an electrode site contralateral to the attention shift minus the ipsilateral site: An 'early directing attention negativity' (EDAN) at posterior sites emerges between 150-400 ms after the cue and has been linked to the initiation of attention shifts (Harter et al., 1989; Hopf & Mangun, 2000; Nobre et al., 2000; but see Van Velzen & Eimer, 2003). The 'anterior directing attention negativity' (ADAN) is observed at frontal and central sites between 300-500 ms after the cue and is thought to be a supramodal attention shift component (Eimer & Van Velzen, 2002; Seiss, Gherri, Eardley, & Eimer, 2007; Van Velzen, Eardley, Forster, & Eimer, 2006; but see Green, Conder, & McDonald, 2008). Finally, the 'late directing attention positivity' (LDAP) at posterior sites starts ~500 ms after the cue and has been linked to changes in excitability in the ventral visual cortex (e.g., Harter et al., 1989).

However, lateralized cue-ERPs are also correlated with the preparation of goal-directed movements (Eimer, Forster, Van Velzen, & Prabhu, 2005; Gherri, Driver, & Eimer, 2008; Gherri & Eimer, 2008; Praamstra et al., 2005; van der Lubbe, Neggers, Verleger, & Kenemans, 2006). For example, van der Lubbe et al. (2006) compared a condition with a central cue for a covert attention shift toward a peripheral location with a condition in which the same cue indicated to prepare a saccade toward that location (which was executed after a second go signal). With that procedure it was shown that similar cue-ERPs arise in both conditions, giving further support to the idea that covert attentional orienting and saccade programming greatly overlap (van der Lubbe et al., 2006; see also Rizzolatti et al., 1987). A critical point in this study (and other studies on cue-ERPs) is that

regardless of whether a spatial cueing procedure cues a covert attention shift or the preparation of an overt response, such as a saccade, MSs are present in both conditions. Importantly, these MSs may comprise overt responses, albeit on a small spatial scale. Thus, in this thesis, we directly related MS dynamics to lateralized cue-ERPs to investigate (1) the link between MSs and the EDAN after a lateralized cue stimulus and (2) the contamination of the ADAN by residual microsaccadic gaze shifts.

*EDAN and the feature-based selection of lateralized cues.* The hypothesis that the posterior EDAN reflects covert attention shifts has been challenged in studies showing that EDAN is instead linked to lateralized aspects of the cue stimulus indicating the direction of these shifts (Jongen, Smulders, & Van Der Heiden, 2007; Van Velzen & Eimer, 2003). In particular, in an ERP study, Van Velzen and Eimer (2003) used a cue arrangement that orthogonally manipulated the hemifield that needed to be attended and the hemifield where the task-relevant cue was presented. As a result, the EDAN depended on the feature-based selection of the relevant cue, but not on the cued attention shift. In particular, while the polarity of the EDAN aligned with the location of the relevant cue, the polarity of the ADAN and LDAP component was still aligned with the direction of the cued attention shift. Thus, Van Velzen and Eimer (2003) concluded that the EDAN rather resembles the N2*pc* component. This component commonly arises in the visual search task at posterior sites contralateral to a target stimulus that is selected among distractors based on its visual features (e.g., Eimer, 1996; Luck & Hillyard, 1994). As we will show in Study 1, MSs also link to feature-based attentional selection. In Study 2, we will

relate this bias in MS orientation directly to the single-trial EDAN/N2*pc* component.

*ADAN and residual corneoretinal artifacts.* Apart from reflecting genuine brain activity linked to the covert deployment of attention (e.g., Yamaguchi et al., 1994), the anterior ADAN component has also been speculated to reflect ocular artifacts from systematic residual eye movements toward the to-be-attended hemifield (e.g., Kennett, Van Velzen, Eimer, & Driver, 2007). As previous studies are not optimized to measure eye movements at the spatial scale of MSs, the contribution of ocular artifacts from MSs to lateralized cue-ERPs is unknown. In general, a microsaccadic gaze shift comprises a movement of the corneoretinal eye dipole which results in a small but reliable corneoretinal (CR) artifact strongest at electrodes of the electrooculogram (EOG; see also Dimigen, Valsecchi, Sommer, & Kliegl, 2009). In Study 2 we investigated if systematic biases in MS orientation toward the to-be-attended hemifield (e.g., Engbert & Kliegl, 2003) lead to a significant scalp lateralization after attention-directing cues at EOG sites. Further we explored how strongly these MS-related CR artifacts propagate to EEG electrodes and mimics or abolishes lateralized components of the cue-ERP.

### 2.3.3 Early modulation of visual processing: The P1 and N1

Instead of relating MSs to stimulus-locked ERPs, it is also possible to investigate how the evoked response time-locked to MSs is affected by attention. In particular, the execution of MSs is accompanied by motor-related activity linked to MS generation and execution, visual activity evoked by the microsaccadic gaze shift, and non-visual (extra-retinal) activity (Martinez-Conde, Otero-Millan, & Macknik,

2013). Of relevance for this thesis is the modulation of MS-related visual activity by visual attention.

In general, gaze shifts from MSs rapidly change the retinal image with similar physiological consequences as when a stationary pattern moves over retinal receptor cells. For example, in intracranial recordings of non-human primates, MSs evoke transient or sustained modulations in in the firing rate of neurons along the visual pathway (e.g., Herrington et al., 2009; Leopold & Logothetis, 1998; Martinez-Conde, Macknik, & Hubel, 2000, 2002; Snodderly, Kagan, & Gur, 2001; reviewed in Martinez-Conde et al., 2013).

In human EEG recordings, a genuine brain response over the posterior cortex is measured after MSs. This **MS-r**elated **p**otential (mSRP) shows a similar P1-N1 complex observed after saccades (e.g., Kazai & Yagi, 2003) and for the visually-evoked potential, that is, the posterior brain response traditionally measured in the EEG after a visual stimulus (Armington & Bloom, 1974; Armington, Gaarder, & Schick, 1967; Dimigen et al., 2009; Gaarder, Krauskopf, Graf, Kropfl, & Armington, 1964). The visual source of the early posterior components after saccadic eye movements is indicated by several findings: These components correlate with the electric response of retinal cells (Armington & Bloom, 1974; Armington et al., 1967), depend on stimulus properties such as luminance and spatial frequency (Armington et al., 1967; Gaarder et al., 1964; Kazai & Yagi, 1999, 2003), and are attenuated or absent when eyes move over homogenous grey or black stimulus patterns (Ossandon, Helo, Montefusco-Siegmund, & Maldonado, 2010). Moreover, source localization studies suggest an origin of the P1 in the striate

and/or extrastriate cortices (Dimigen et al., 2009; Kazai & Yagi, 2003). Thus, the P1 has been interpreted in terms of a transient feed-forward activation of the visual cortex after (micro-)saccadic shifts of the retinal image (e.g., Dimigen et al., 2009).

Importantly, in a recent study the visual response after MSs has been related to attention: When covert attention is deployed toward a peripheral target location, the P1 and N1 of the mSRP showed enhanced responses for attended compared to unattended stimuli (Meyberg, 2011). A similar finding has been observed for the visually-evoked potential for an attended stimulus when compared to an unattended stimulus and is likely mediated by recurrent top-down signals from the frontoparietal network (e.g., Van Voorhis & Hillyard, 1977; reviewed in Eimer, 2014; Hillyard & Anllo-Vento, 1998). Study 3 aimed at further exploring the nature of this mSRP enhancement effect by investigating its temporal evolution. In addition, we tested whether attention effects of the mSRP arise through the mere overlap of lateralized posterior cue-ERPs that are present in the same time window.

# 3 Summary of results

## 3.1 Overview of the thesis

Based on the state-of-the-art research outlined above this thesis investigated MSs in spatial cueing tasks to address two **major research objectives**:

First, we aimed at advancing our knowledge on the link between MSs and endogenous attention. We hypothesized that if the generation of MSs is integrated into the neural network in control of visual attention, correlations of MS dynamics with mechanisms of attentional selection and their associated neural correlates should be observed. We therefore focused on dissociating the effects of location-based and feature-based selection of visual stimuli during spatial cueing of attention and related MSs to ERP correlates of visual attention.

Second, we investigated if ERP correlates of visual attention are caused by the mere temporal overlap of two sources of EEG activity: the lateralized ERP components observed after am attention-directing cue (e.g., Harter et al., 1989) and the synchronized EEG activity after involuntary MSs that occur with great temporal jitter relative to the cue (e.g., Gaarder et al., 1964). In principle, possible contaminations of attention-related ERP effects are reciprocal. For example, ocular artifacts from MSs could mimic or abolish effects observed for the cue-ERP. Likewise, the components of the cue-ERP could also modulate the effects of visual attention observed for MS-related brain potentials.

To this end, two experiments were conducted in which participants performed a spatial cueing task that required an endogenous shift of covert attention. In both experiments, EEG and eye movements were co-registered. In the first experiment, we presented a spatial cue of the kind used by Van Velzen and Eimer (2003) that allows dissociation of lateralized aspects of the cue stimulus (feature-based attention) from the direction of the attention shift initiated by that cue (location-based attention). The results from the ET recording are detailed in Study 1 and the co-registered ERP and ET data are presented in Study 2. In the second experiment, we closely followed the procedure by Engbert and Kliegl (2003) and presented a single arrow cue at screen center that pointed left or right. These data are presented in Study 3.

**Study 1** investigated how MS orientation is affected by the cued shift of covert attention and the selection of lateralized aspects of the cue stimulus and how biases in MS orientation are linked to response times. In addition, both selection mechanisms were implemented in a computational model on the generation of MSs (e.g., Engbert, 2012).

**Study 2** focused on the coupling between MSs and lateralized cue-ERPs. The main purpose was to test if biases in MS orientation co-vary with the posterior EDAN/N2*pc* which has previously been shown to be feature-selective for lateralized aspects of the cue (Van Velzen & Eimer, 2003). Further, we investigated if CR artifacts from MSs contaminate the measurement of lateralized cue-ERPs, in particular the frontal ADAN.

**Study 3** examined the effect of covert attention on MS-related visual brain potentials; specifically, the attention-related enhancement of the posterior P1 and N1 component of the mSRP. The main goal was to investigate how these attention effects evolve over time. In addition, we investigated if attention effects of the mSRP are caused by lateralized posterior cue-ERPs that are present in an overlapping time interval.

## 3.2 Study 1: Microsaccades and the selection of visual stimuli

Meyberg, Sinn, Engbert, and Sommer (2017): Revising the link between microsaccades and the spatial cueing of voluntary attention. *Vision Research, 133(2017),* 47-60.

***Research questions and method.*** Study 1 tested the hypothesis that when covert attention is cued using a lateralized cue stimulus, MSs may not only align with the attention shift toward the to-be-attended hemifield (location-based attention), but also (or instead) with the feature-based selection of lateralized aspects of this cue (feature-based attention). To this end, we used a cue stimulus modeled after Van Velzen and Eimer (2003) that manipulated the to-be-attended hemifield independently of the hemifield in which the relevant cue was presented: Two arrowheads were presented to the left and right of the fixation point. The arrows differed in color (red vs. blue), pointed toward opposite hemifields (< > vs. > <), and only one arrow was task-relevant (coded by arrow color) and indicated the likely target location. In a control condition with *congruent cues* (< >), the cue was presented in the to-be-attended hemifield. Thus, this condition resembled previous

cueing studies in which, for example, the tip of a left-pointing central arrow cue is presented in the left hemifield (e.g., Engbert & Kliegl, 2003). In the critical condition with *incongruent cues* (> <), the cue appeared in the hemifield opposite to the one that needed to be attended. If MSs align with the cued attention shift, we expected a bias toward the to-be-attended hemifield with both cue arrangements. If, however, MSs dominantly align with the relevant arrowhead, we expected a movement bias away from the to-be-attended hemifield with incongruent cues. We further examined the link between cue-related biases in MSs and subsequent response times that has been reported previously (e.g., Laubrock et al., 2010) in light of a possible effect for the feature-based selection of the cue stimulus.

Finally, we simulated MS behavior during spatial cueing in a recent computational model (Engbert, 2012; Engbert et al., 2011). Therefore, we implemented both attentional selection mechanisms, the location-based selection of the to-be-attended target location and the feature-based selection of the lateralized cue, based on attention-related changes in SC activity (e.g., Fecteau et al., 2004; Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Kustov & Robinson, 1996; McPeek & Keller, 2002). This procedure allowed us to isolate both selection mechanisms and to explore their temporal dynamics and the strength with which they affect MS generation.

***Summary of study.*** The orientation of MSs was aligned with the cueing conditions during the rebound interval in the MS rate. After congruent cues, we replicated the orientation bias toward the to-be-attended hemifield (e.g., Engbert & Kliegl, 2003) and the finding of facilitated reaction times (RTs) in trials with a MS oriented

toward the target (e.g., Laubrock et al., 2010). However, the condition with incongruent cues revealed that both results depended on a link between MSs and lateralized aspects of the cue rather than a link between MSs and the cued attention shift. In particular, after incongruent cues, more MSs were oriented away from the to-be-attended hemifield but toward the location of the relevant cue. Likewise, we observed slower RTs in trials with a MS oriented toward the target. Congruently, when we directly investigated the classical spatial cueing effect on RTs, that is, when we subtracted RT in trials with invalid cues from RT in trials with valid cues (e.g., Posner, 1980), we observed stronger cueing benefits in trials when a MS was directed toward the relevant cue regardless of cue arrangement.

Despite the dominant preference of MSs to move toward the relevant cue, we still observed a reliable alignment with the cued attention shift. This finding was confirmed when we isolated the effects of location- and feature-based attention by running numeric simulation in a computation model: Both selection mechanisms modulated the orientation of 'rebound' MSs, with the impact of feature-based selection being four times stronger than the impact of location-based selection.

***Gain in knowledge.*** Study 1 shows that lateralized visual cues trigger a location-based selection of the to-be-attended target location and a feature-based selection of task-relevant aspects of the cue stimulus. Although MSs were related to both selection mechanisms, they dominantly aligned with the feature-based selection of the cue. This finding suggest that at the level of the SC two attentional mechanisms operate in parallel and jointly determine MS dynamics during spatial cueing of attention with lateralized cue stimuli.

## 3.3 Study 2: Microsaccades and lateralized cue-ERPs

Meyberg, Sommer, and Dimigen (2017): How microsaccades relate to lateralized ERP components of spatial attention: A co-registration study. *Neuropsychologia, 99(2017),* 64-80.

***Research questions and method.*** Study 2 examined the link between MSs and lateralized ERPs that are elicited after an attention-directing cue, focusing on two particular aspects: (A) We investigated a possible functional coupling between biases in MS orientation and the posterior EDAN/N2*pc*. The feature-selectivity for lateralized cue stimuli observed for MSs in Study 1 has also been reported in a previous ERP study for the EDAN/N2*pc* component (Van Velzen & Eimer, 2003). Thus, in Study 2, we directly related MS behavior to the EDAN/N2*pc* on a single-trial level. We expected to observe a stronger EDAN/N2*pc* in trials in which a MS moved toward the relevant cue, while EDAN/N2*pc* might be reduced or absent in trials with a MS moving away from that cue. (B) Second, we investigated whether cue-ERPs, in particular the frontal ADAN are contaminated by CR artifacts caused by microsaccadic movements of the eye dipole. To this end, we compared a dataset that was corrected for ocular artifacts by *independent component analysis* (ICA; Jung et al., 2000; Makeig, Bell, Jung, & Sejnowski, 1996) with the uncorrected version of that dataset.

***Summary of study.*** In Study 2 we show that systematic cue-related biases in MS orientation are directly related to lateralized cue-ERPs. (A) MSs were coupled to the posterior EDAN/N2*pc*. In particular, MSs and EDAN/N2*pc* were more strongly aligned with the lateralized aspects of the cue rather than the direction of the cued attention shift in an overlapping time interval after the cue. Importantly, this

coupling was present even on a single-trial level: We observed stronger EDAN/N2*pc* in trials with MSs moving toward the relevant cue, while EDAN/N2*pc* was absent with MSs moving opposite that cue. (B) We further find that MSs were accompanied by small CR artifacts (average amplitude below 3 $\mu$V) that were strongest at the horizontal EOG but also propagated to frontal electrodes (see also Dimigen et al., 2009). These MS-related CR artifacts followed the cue-related bias in MS orientation and could be fully eliminated with ICA correction. Importantly, applying ICA-correction also eliminated the frontal part of the ADAN component, while ADAN at central sites was still present.

***Gain in knowledge.*** Study 2 shows that, on the one hand, MSs are a neglected source of artifacts in ERP studies. Importantly, if MS characteristics such as orientation are systematically correlated with experimental factors, MS-related ocular artifacts can mimic or eliminate ERP effects (see also Yuval-Greenberg et al., 2009). On the other hand, the results indicate that MSs may be seen as overt responses during covert orienting that are functionally linked to neural correlates of attention. The coupling of MSs and the EDAN/N2*pc* suggests that both variables reflect activity in the neural network for selecting stimuli based on their visual features and orienting behavior toward selected stimuli.

## 3.4 Study 3: Microsaccade-related potentials and covert attention

Meyberg, Werkle-Bergner, Sommer, and Dimigen (2015). Microsaccade-related brain potentials signal the focus of visuospatial attention. *Neuroimage, 104*, 79-88.

***Research questions and method.*** Analyses in Study 3 are based on the data of a previous study by Meyberg (2011) that utilized a spatial cueing task with a central arrow cue pointing left or right. In that study, we found that visual brain potentials after MSs are enhanced for stimuli covered by the focus of attention. In particular, the posterior P1 and N1 component of the mSRP were stronger over scalp sites contralateral to the to-be-attended hemifield. Study 3 aimed to investigate these lateralization effects of the mSRP from two perspectives: (A) We investigated if the lateralization of the mSRP with attention follows the temporal dynamics well-established for endogenous spatial attention (Müller & Rabbitt, 1989). To this end, the lateralization of the mSRP for the P1, N1, and the P1-N1 difference was calculated in successive time windows relative to the cue. We further compared the temporal profile of attention effects on the mSRP with the temporal profile observed for attention effects on MS orientation. (B) We tested the hypothesis that the lateralization of the mSRP with attention does not reflect an attention-related enhancement of visual processing, but is rather caused by lateralized cue-evoked ERPs that add to the mSRP effect. To this end, we investigated whether attention effects on mSRPs were present even if the average cue-ERP was subtracted from the single trial EEG response.

***Summary of study.*** During covert orienting, microsaccadic gaze shifts were followed by an mSRP with a typical signature comprising a P1-N1 complex at posterior sites, and a spike potential (SP) and CR artifacts at EOG sites. Moreover, the mSRP was modulated by attention with stronger P1 and N1 over scalp sites contralateral to the to-be-attended hemifield. In addition, MS orientation affected

the mSRP such that stronger P1 and N1 were observed over scalp sites ipsilateral to movement direction. The effects of covert attention and MS orientation on the mSRP were strictly additive (see also Meyberg, 2011).

With respect to our research questions we find: (A) The lateralization of the mSRP showed a consistent pattern with all three markers, the P1, N1, and the P1-N1 difference. While the mSRP was not lateralized during the baseline interval, component enhancement with attention built up between 150-300 ms after the cue. This interval corresponds with the interval when MSs moved toward the to-be-attended hemifield (i.e., between 200-400 ms post-cue). Following this initial build-up, enhancement was stable prior to target occurrence. In contrast, no systematic MS bias was observed in that late interval.[1] (B) After the cue, we observed a reliable lateralization of the cue-ERP (data not shown in the article). Most prominent at posterior sites was a positive deflection contralateral to the cued attention shift, the LDAP component. Subtracting the average cue-ERP did not change the overall pattern of results, that is, we still observed a reliable enhancement of the mSRP with attention.

***Gain in knowledge.*** Study 3 shows that the lateralization of the mSRP towards the focus of attention that is observed after an attention-directing cue is not a mere artifact caused by overlapping cue-evoked activity. Instead, the temporal profile of

[1] Running the same temporal analysis for the effect of MS orientation on the mSRP revealed that this effect was unaffected by the spatial cueing procedure (data not shown in the article). In particular, the orientation-related lateralization of the mSRP was observed in the baseline and cue-target interval.

this lateralization effect resembles the temporal dynamics of attention-related changes in visual sensitivity (e.g., Müller & Rabbitt, 1989) and links this effect to a gain-control mechanism (e.g., Hillyard et al., 1998). In contrast, the orientation bias in MSs early after cue onset are more likely related to the transient activation pattern in the SC that arise with shifts of covert attention and/or the feature-based selection of stimuli (e.g., Fecteau & Munoz, 2006). The additional lateralization of the mSRP by the orientation of a MS may reflect a systematic displacement of the foveal visual stimulation into one hemifield.

# 4 Discussion and integration of results

The study of the cognitive and neural mechanisms of visual attention has greatly benefited from integrating results obtained with behavioral and neuroscientific methods. However, little attention has been paid to the now well-established finding from eye tracking studies showing a tight correlation of MSs to covert attention. Instead, the absolute majority of neuroscientific studies still assumes that the deployment of covert attention occurs in the absence of eye movements. To bridge this gap, the present thesis combined eye movement and ERP recordings in a classical task of covert attention, that is, the Posner spatial cueing task.

A major research goal was to investigate the relation between MSs and endogenous covert attention. Emphasis was placed on dissociating the effects of location-based and feature-based selection of visual stimuli during spatial cueing of attention and to relate MSs to ERP correlates of visual attention. We further explored the temporal profile of the gain-modulations on MS-related brain responses. As a further goal, we assessed a possible contamination of attention-related ERP effects. This contamination may be produced by overlapping electrical responses related to the presentation of stimuli and the occurrence of MSs. In the following, the results we obtained to address both research goals are discussed separately, and limitations and further directions will be discussed along the way.

## 4.1 Microsaccades and visual attention

### 4.1.1 Microsaccades reflect location- and feature-based visual selection

The question whether MSs relate to attention has led to controversial debates (Horowitz, Fine, Fencsik, Yurgenson, & Wolfe, 2007; Laubrock et al., 2007; Rolfs, Engbert, & Kliegl, 2004; Tse, Sheinberg, & Logothetis, 2002, 2003, 2004). For example, high rates of stimulus presentation suppress MS generation, probably eliminating directional correlations of MSs with attention in change blindness tasks (Rolfs et al., 2004; Tse et al., 2004). In contrast, MS alignment with covert attention is now well-established in the Posner spatial cueing task (e.g., Engbert & Kliegl, 2003; Hafed & Clark, 2002; Laubrock et al., 2005; Tian et al., 2016) and has been shown to be very strong for endogenous attention (Laubrock et al., 2010; Pastukhov & Braun, 2010). Using an arrow cue, Laubrock et al. (2010) reported a directional selectivity of MSs toward the to-be-attended hemifield in 75% (up to 90%) of cases depending, for example, on the time interval of MS occurrence (i.e., it was stronger for 'rebound' MSs). Thus, these transient biases in MSs have been suggested to reflect shifts of covert attention initiated by the spatial cue (Laubrock et al., 2010).

In Study 1 and 2, we used a similar spatial cueing task to Laubrock et al. (2010), but our cue stimulus additionally allowed us to dissociate effects associated with the cued attention shift and the selection of the lateralized cue stimulus. On a general level, we report further evidence for a tight coupling between visual attention and MSs during the rebound interval. However, we show that 'rebound' MSs are determined by the combined effects of two attentional selection mechanisms that overlap in time: the location-based selection of the to-be-attended

target location and the feature-based selection of task-relevant aspects of the lateralized cue. This is a noteworthy finding as the latter effect has been overlooked in previous studies with lateralized cues and, therefore, challenges some conclusions drawn in these studies (e.g., Engbert & Kliegl, 2003; Laubrock et al., 2010). In what follows, the link of 'rebound' MSs to location- and feature-based selection will be discussed in separate sections.

***'Rebound' microsaccades and the feature-based selection of stimuli.*** In a spatial cueing task, a central cue instructed a covert attention shift toward one hemifield. The cue consisted of distinct stimulus parts of different color, of which only the stimulus part displayed in the task-relevant color indicated the to-be-attended hemifield. With this cue, we show that MSs are coupled to the attentional selection of stimuli based on their visual features:

First, in Study 1 and 2 we show that MSs dominantly moved toward the relevant part of the cue rather than toward the irrelevant one; a movement bias that was present even if it required a gaze shift away from the to-be-attended hemifield. This correlation of MSs with feature-based attention is largely consistent with the role of saccadic eye movements. In many everyday situations, prior knowledge about the location of relevant objects is not given, but their features are often known, for example, when one is looking for a yellow cab on a crowded street. With unconstrained viewing conditions, gaze frequently shifts across the scene and inspects different objects to investigate their match with the desired feature (*overt search*). Nonetheless, studies implementing *covert search* share the general assumption also made in studies on covert attentional orienting; that is, covert

search can be performed in the absence of eye movements (e.g., Klein & Farrell, 1989). Along these lines, it has been shown that covert search follows similar pattern as overt search (Klein & Farrell, 1989; Maioli, Benaglio, Siri, Sosta, & Cappa, 2001; Nothdurft, Pigarev, & Kastner, 2009; Zelinsky & Sheinberg, 1997). This result, however, does not imply that fixational eye movements, in particular, MSs are not related to and do not contribute to the covert search process. Instead, in the present thesis, we show that MSs align with feature-based attention even if only one of two foveally presented arrowheads needs to be selected.

We speculate that directing gaze toward the relevant cue serves to improve the perceptual processing of this stimulus, a function also ascribed to saccades during overt search. These MS-related perceptual changes may be based on two mechanisms: (1) Microsaccadic gaze shifts may optimize the foveal location of the relevant cue stimulus allowing in-depth perceptual processing. In fact, this oculomotor strategy has been ascribed to MSs in recent studies that required high-visual acuity judgements during fixation (Ko, Poletti, & Rucci, 2010; Poletti, Listorti, & Rucci, 2013). Likewise, even during free exploration and overt search of complex scenes, small saccades with amplitudes below 1° are present. These MSs share several kinetic characteristics with saccades (but see Mergenthaler & Engbert, 2010) and are especially frequent close to the regions of identified targets (Otero-Millan, Troncoso, Macknik, Serrano-Pedraza, & Martinez-Conde, 2008). (2) In addition, processing the cue stimulus could benefit from changes in visual processing that occur time-locked to MS generation and depend on movement direction (reviewed in Hafed et al., 2015). For example, shortly before a

(micro)saccade, visual sensitivity increases at the location this eye movement is prepared toward (e.g., Castet et al., 2006; Deubel & Schneider, 1996; Hafed, 2013; Tian et al., 2016). Importantly, this effect is not restricted to stimuli presented at the subsequent saccade goal. In case of MSs, enhanced visual representations have been observed for stimuli more eccentric than the landing position of the MS (e.g., Hafed, 2013). On a neural level, improved sensitivity for a stimulus before a MS is linked to stronger visual burst of neurons in the SC and frontal eye fields (Chen et al., 2015). Such effects have been interpreted as the consequence of a 'corollary signal', which represents a copy of the actual motor preparatory signal that is sent to other areas to inform about the pending eye movement (Chen et al., 2015; Hafed et al., 2015; see also Wurtz, 2008). To summarize, the systematic bias of MSs toward the lateralized cue stimulus in Study 1 and 2 suggests that MSs may be seen as an overt saccadic response during the 'covert' selection of this stimulus.

Second, in Study 2, we further show that MS occurrence and alignment with the relevant cue was coupled to the posterior EDAN/N2*pc*, an ERP component of the feature-based selection of stimuli (Luck & Hillyard, 1994; Van Velzen & Eimer, 2003) that is likely generated in the ventral visual cortex (Hopf, Boelmans, Schoenfeld, Heinze, & Luck, 2002; Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004). This finding has two important implications: (1) The microsaccade-ERP coupling might be mediated by a direct pathway from higher visual areas to the SC. MSs have been linked to cognitive processes in the past (e.g., reviewed in Rolfs, 2009), however, it is unknown how cortical areas contribute to the generation of MSs (see also Hafed, 2011). Thus, the link between MSs and the EDAN/N2*pc*

observed even on a single-trial level might be first evidence toward such a cortico-subcortical connection. Alternatively, the present correlation may be mediated by frontal and/or parietal cortical areas involved in attention (e.g., Corbetta & Shulman, 2002); thus, the exact pathway underlying this microsaccade-ERP coupling needs to be explored in future studies. Nonetheless, the present finding suggests that the same network or greatly overlapping neural networks are activated for selecting the relevant stimulus (reflected in the EDAN/N2*pc*) and for generating a gaze shift toward the selected stimulus (Corbetta, 1998; Corbetta & Shulman, 2002; Fecteau & Munoz, 2006; Krauzlis et al., 2013). (2) The present data also reveal an important difference in how EDAN/N2*pc* and MSs relate to attention: The EDAN/N2*pc* depended on the location of the lateralized cue, but not on the direction of the cued attention shift (see also Van Velzen & Eimer, 2003). MSs during the rebound interval were related to both, the selection of the lateralized cue and the cued attention shift. Moreover, MSs occurring later in the cue-target interval rather served other oculomotor needs but not attention (Laubrock et al., 2010; Tian et al., 2016). This pattern supports the claim that EDAN/N2*pc* exclusively reflects spatially specific neural activity during the selection stage of a target based on visual features (Luck & Hillyard, 1994). In contrast, MSs are directly related to the activity of the SC that has a crucial role not only in mediating bottom-up demands, but also in integrating different top-down demands such as the location- and feature-based selection of stimuli (e.g., Krauzlis et al., 2013; Munoz & Everling, 2004; discussed also in the following).

A clear limitation of the experimental procedure in this thesis is that the link between MSs and feature-based selection was not addressed in isolation, but in a task that also required a cued shift of covert attention. Thus, to allow further generalization from our results, it is necessary to directly investigate MS behavior, for example, in the visual search task (Treisman & Gelade, 1980). This could help to resolve the discrepancies between the present results and the results from a previous study investigating MSs in a visual search task (Turatto, Valsecchi, Tame, & Betta, 2007)[2] by determining the conditions under which MSs relate to feature-based attention. Indeed, we speculate that investigating MSs during covert search will be a fruitful future research agenda by addressing, for example, the following questions: Do MSs exhibit a similar search pattern during covert search as saccades during overt search? Is the MS alignment with the target based on a correlation of MSs with a covert shift of attention that has been suggested to occur during covert search? What is the temporal dependency of target selection and MS generation? Do MSs distinguish between serial and parallel processing modes during covert search? What are the visual features that MSs are feature-selective for?

[2] In the study by Turatto et al. (2007), a color singleton had to be selected among distracting items arranged on an imaginary circle of 10°. In contrast to our findings, Turatto et al. (2007) did not observe a MS bias toward the selected target (the target resembles the relevant cue in our study). However, in line with our results, MSs moved away from the target in an interval between 500 to 700 ms after search array onset. This late effect depended on task-demands, that is, it was observed in a more difficult condition when the shape of the color singleton had to be discriminated, but not if the singleton just had to be detected. There are several differences with respect to stimulus arrangements and task-related procedures between our study and the study by Turatto et al. (2007) that might have contributed to different results. However, we suggest that a good starting point for dissolving the conflicting results would be to investigate how stimulus eccentricity and target selection mode (bottom-up vs. top-down selection) modulate the link between MSs and feature-based attention.

***'Rebound' microsaccades and the location-based selection of stimuli.*** When we controlled for the feature-based selection of the relevant cue in Study 1 and 2, we replicated a bias of MSs with the direction of the cued attention shift (e.g., Engbert & Kliegl, 2003; Laubrock et al., 2010). However, this latter bias was four times weaker than the first bias. Thus, this finding of a dominant bias toward the relevant cue but not toward the to-be-attended target location suggests that the correlation of MS orientation with covert attention is likely overestimated in studies with lateralized cues. In particular, the majority of previous eye tracking studies used different versions of the *congruent cue* in Study 1 and 2, that is, the task-relevant parts of the cue were presented in the to-be-attended hemifield. In particular, these studies used conventional central arrow cues (e.g., in Study 3; see also Engbert & Kliegl, 2003; Hermens & Walker, 2010; Horowitz et al., 2007; Laubrock et al., 2007, 2010; Wieczorek, 2016), but also indicated the target location with the highlighted arm of a central fixation cross (Pastukhov & Braun, 2010), a color singleton among of four peripheral rings (Hafed et al., 2011, 2013), or a flickering peripheral box (Pastukhov, Vonau, Stonkute, & Braun, 2013). With such lateralized cues, a feature-based selection of relevant stimulus aspects is probably initiated and MSs that are actually aligned with the lateralized cue may erroneously be interpreted as being aligned with the covert attention shift.

In light of this possible confounding effect by stimulus arrangement, it is not surprising that the strongest correlations of MSs with covert attention have been reported in studies with lateralized cues. In fact, with non-lateralized symbolic color cues, MS biases toward the to-be-attended hemifield were either weaker and

delayed when compared to a condition with arrow cues (Engbert & Kliegl, 2003) or even absent (Laubrock et al., 2005). In contrast, two studies with lateralized cues reported a directional selectivity of MSs with attention in 75% or up to 98% of cases (Laubrock et al., 2010; Pastukhov & Braun, 2010). Discrepancies between these studies may depend on the general efficiency of a cue to trigger covert shifts of attention (see also Engbert & Kliegl, 2003) and other experimental factors that are thought to modulate the strength of the microsaccades-attention link, for example, response modality (Laubrock et al., 2010) or attentional load (Pastukhov & Braun, 2010). Nonetheless, future research should test if these very high correlations after lateralized cues are based on an alignment of MSs with covert attention or with lateralized parts of the cue stimulus. Therefore, we suggest also implementing a condition for estimating the effect of the feature-based selection of the cue. This can be done, as in Study 1 and 2, by manipulating the shape of the cue stimulus (e.g., congruent cue: <> vs. incongruent cue: ><), but keeping the instruction constant (if the relevant arrow points left, attend left). Alternatively, one can present the same cue (e.g., left-pointing central arrow), but change the instruction trial-wise or block-wise (e.g., congruent cues in block 1: if the arrow points left, attend left vs. incongruent cues in block 2: if the arrow points left, attend right; for a similar procedure with exogenous cues see also Hafed & Clark, 2002). With this latter procedure it would also be possible to test if processing of certain cue types, for example, gaze cues, also has a (neglected) lateralized component. In particular, one could speculate that if a gaze cue points left, the left eye of the gaze cue is selected over the right eye (and vice versa for gaze cues pointing right). Thus, it would be

interesting to test if the previous finding of a MS bias toward the to-be-attended hemifield after gaze cues (Yokoyama et al., 2012) is based on a movement alignment with covert attention or with the eyes of the cue.

### 4.1.2 Models on microsaccade dynamics and visual attention

The alignment of MSs with location- and feature-based attention is in line with the notion of a neural network that selects stimuli based on their location and features, and integrates task-relevant information to guide goal-driven behavior. Previous electrophysiological and neuroimaging studies suggest that this complex function is accomplished by a network of frontoparietal as well as subcortical structures including the SC (Corbetta et al., 2008; Corbetta & Shulman, 2002; Fecteau & Munoz, 2006; Krauzlis et al., 2013).

The central role of the SC in mediating the microsaccade-attention coupling is supported by three findings: First, MSs are generated in the deeper layers of the rostral pole of the SC (e.g., Hafed et al., 2009; Hafed & Krauzlis, 2012). In particular, the SC contains a topographic map of visual space where foveal and more eccentric spatial locations are confined to neurons of the rostral and peripheral SC, respectively. For the visual neurons of the superficial layer of the SC, this map encodes stimulus location. In the deeper layers, motor and visuomotor neurons organize movement-related activity toward respective locations. Given this topographic motor map, MSs and small saccades are generated in the rostral SC and larger saccades at more peripheral parts of the SC (e.g., Hafed et al., 2009; Robinson, 1972; e.g., reviewed in Munoz & Everling, 2004; Hafed, 2011). Second, neurons of the peripheral SC show distinct but spatially selective activity pattern

for location- and feature-based attention (e.g., Fecteau et al., 2004; Kustov & Robinson, 1996; reviewed in Krauzlis, Lovejoy, & Zenon, 2013). Third, there is evidence for a coupling mechanism between neurons of the peripheral SC that are spatially selective for the to-be-attended location and the rostral SC involved in MS generation, as suggested by a recent spatial cueing study in monkeys. In particular, if these neurons of the peripheral SC are temporarily deactivated, the link between MS orientation and covert attention can be disrupted although the general ability to direct a MS toward the to-be-attended location remains intact (Hafed et al., 2013).

Based on these findings, attention-related changes in SC activity have been implemented in computational models to account for cue-related biases in MSs (Engbert, 2012; Hafed et al., 2009). In the following, the results of this thesis will be integrated into the model by Engbert (2012) and an alternative account on the microsaccades-attention coupling will be discussed (e.g., Hafed et al., 2015).

***A computational model on microsaccades and attention.*** Recently, Engbert and colleagues have proposed a comprehensive model that provides an integrated account on the generation of MSs and fixational drift (Engbert et al., 2011) and can explain the modulation of MS rate by sensory transients and the correlations of MS orientation with exogenous and endogenous attention (Engbert, 2012)[3]. In brief, the

[3] Two further models on the microsaccade-attention coupling have been proposed (Hafed et al., 2009; Tian et al., 2016). The model by Hafed et al. (2009) generally aims at simulating MS generation based on SC functioning. The modelling strategy for attention effects is limited to a mechanism that generates MS biases within their framework. The model by Tian et al. (2016) simulates MS dynamics after exogenous cues (see also Hafed et al., 2015). In the next section, the basic assumptions of this model are presented and the suitability of this account to explain MS dynamics with endogenous attention will be evaluated.

model generates slower fixational drift as a consequence of random motion on a lattice with a preference for new lattice sites (i.e., self-avoiding walk; Freund & Grassberger, 1992). The lattice represents the topographic map of the SC and the random motion principle likely serves to refresh representations of retinal receptor cells. During the self-avoiding walk, MSs are triggered by a threshold mechanism (Engbert et al., 2011).

An important component of the model is a movement potential that spatially constraints the random motion on the lattice and can be thought of as the top-down intention to maintain fixation. Moreover, temporal variations of the potential slope have been used to simulate changes in the peripheral SC with attention (e.g., Ignashchenkova et al., 2004). More specially, an asymmetric widening of the movement potential toward one side, for example, the to-be-attended side, drives MS biases toward that side (Engbert et al., 2011; Engbert, 2012).

In Study 1, we simulated MS behavior observed after a lateralized endogenous cue in the model by Engbert and colleagues. To account for the combined effects of location- and feature-based selection, two attention mechanisms were implemented that affected the slope of the movement potential by mimicking the distinct activity pattern of the SC with attention: Following Engbert (2012), location-based attention was simulated as a unilateral widening of the potential toward the locus of attention. This relates to the increased activity of neurons of the peripheral SC representing the to-be-attended location (Ignashchenkova et al., 2004; Kustov & Robinson, 1996). In contrast, with feature-based attention, we allowed both sides of the potential to vary, which resulted in a relative potential widening toward the side

where the relevant cue was presented. This model behavior resembles the finding in visual search tasks that SC activity increases at all possible target locations during the feed-forward processing of the search array. An enhanced response for the actual target arises during a subsequent recurrent processing stage (e.g., McPeek & Keller, 2002, 2004).

Thus, although the effect of feature-based attention has not been addressed in the previous simulation study by Engbert (2012), we show that the model by Engbert and colleagues can be extended based on principles that are neurophysiologically plausible. Interestingly, despite the distinct implementations for the effect of location- and feature-based attention on the movement potential, both mechanisms exhibited spatially selective modulations for the to-be-selected stimulus. At the level of the SC, this suggests that the same coupling mechanism observed for location-based attention (Hafed et al., 2013) may exist for mediating the effect of feature-based attention. Alternatively, it is possible that such a coupling mechanism is not needed with the present stimulus configuration, since the cue was presented within the foveal region and, thereby, might have been the planned endpoint of the MS. Thus, the neural underpinning of the effect of feature-based selection needs to be tested in future studies. For example, a simple manipulation would be to test if MSs are feature-selective only for a foveal stimulus as presented in our task or also for peripheral stimuli (which suggests that a coupling mechanism is involved).

***An alternative account for exogenous attention.*** In a series of experiments with peripheral exogenous cues, Hafed and colleagues have recently proposed an alternative account of the link between MSs and visual attention based on two

assumptions (Hafed, 2013; Hafed et al., 2015; Tian et al., 2016). First, MSs are generated by an oscillatory process which controls foveal fixation error. The presentation of a peripheral cue resets this ongoing process and biases it toward the cue's location, which results in the well-known alignment of MSs with the cue (e.g., Galfano et al., 2004; Laubrock et al., 2005; Tian et al., 2016). Second, MS generation is associated with peri-microsaccadic changes in visual sensitivity, such as improved perceptual processing briefly before MSs (Hafed, 2013). Thus, Hafed and colleagues claim that facilitatory and inhibitory visual effects commonly associated with covert attention result from the generation of a MS toward or away from a stimulus, respectively (e.g., Tian et al., 2016).

In line with their second assumption, there is now growing evidence of improved visual processing before MSs (Chen et al., 2015; Hafed, 2013; Hafed et al., 2011; Tian et al., 2016; Yuval-Greenberg, Merriam, & Heeger, 2014) and these attention-like effects do not depend on spatial cueing procedures, but also occur during simpler fixation tasks (e.g., Tian et al., 2016; Yuval-Greenberg et al., 2014). In the following, I will review recent experimental data provided by Hafed and colleagues in support of their first assumption, which addresses the effect of spatial cueing on MSs that occur later in the cue-target interval:

In general, MSs show task-related modulations also after the early cue-related biases. However an alignment of late MSs with the to-be-attended hemifield (or with the location of the lateralized cue) has only been observed in a study with a fixed cue-target interval (Pastukhov & Braun, 2010), but not in studies with variable intervals (see Study 1 and 3; e.g., Engbert & Kliegl, 2003). Instead, in those studies,

MSs tend to move back and forth along the meridian or diagonal at which the target is expected to occur (Hafed, 2013; Hafed et al., 2011; Hermens & Walker, 2010; Pastukhov et al., 2013; Tian et al., 2016).

There is some dispute over the meaning of this late oscillatory pattern. For example, this effect has been related to aspects of sustained attention (Hafed et al., 2011; Pastukhov et al., 2013). Alternatively, MSs may generally be triggered by basic oculomotor needs, such as to prevent visual fading (Ditchburn, 1980; Engbert & Mergenthaler, 2006; Martinez-Conde, Macknik, Troncoso, & Dyar, 2006; McCamy, Macknik, & Martinez-Conde, 2014; but see Poletti & Rucci, 2016) or to maintain fixation (Cornsweet, 1956; Engbert & Kliegl, 2004). Thus, as participants are asked to maintain fixation in spatial cueing tasks, this late movement pattern may correct for fixation errors introduced by earlier cue-related biases (Laubrock et al., 2010; Tian et al., 2016) or for the covert attention shift that is mistakenly perceived as an overt eye movement (Laubrock et al., 2005). Strong evidence for a basic oculomotor function of late MSs comes from a study by Hafed and colleagues using a retinal stabilization technique that allows the immobilization of stimuli on the retina and, thereby, the correction of the fixation error introduced by MSs and fixational drift (Tian et al., 2016). With this procedure, the oscillatory movement pattern after exogenous cues could be eliminated.

Importantly, Hafed and colleagues interpret this latter finding in favor of their first assumption, namely that MSs during spatial cueing solely serve to reduced fixation errors. This interpretation is at odds with the data presented by Tian et al. (2016) in several respects: First, applying the retinal stabilization technique affected MS

behavior not earlier than 350 ms post-cue. The well-established early cue-related biases – toward the to-be-attended hemifield (attentional capture) and then away from this hemifield (inhibition of return; e.g., see Galfano et al., 2004) – were preserved. While the presence of the first bias is predicted by their account in terms of the initial cue-related reset of the ongoing generation of MSs, the second bias should have been eliminated in a condition with a stabilized retinal image. In particular, according to Hafed and colleagues, the purpose of this second bias is to correct for the fixation error introduced by the first movement bias which directed gaze toward the to-be-attended location and, thereby, away from central fixation. Second, visual inspection of their data reveals that the first bias (attentional capture) even seemed to be (numerically) enlarged when compared with a condition without retinal stabilization of stimuli (see Fig. 12; Tian et al., 2016). Finally, a sustained movement bias away from the location of the cue emerged after 350 ms post-cue in the stabilized condition, well in line with the finding that the effect of inhibition of return can last up to 3 s (reviewed in Samuel & Kat, 2003). In sum, these results suggest that the early cue-related biases do not (primarily) reflect oculomotor correction, but rather other processes such as attention, and that the close correlation of MS biases with perceptual performance after exogenous cues instead reflects a coupling of both phenomena with attention.

In their paper, Hafed and colleagues further speculate that a similar account also holds true for endogenous attention (Tian et al., 2016). However, a model of endogenous attention that completely bypasses higher-level processing may be invalid for at least two reasons: First, for exogenous attention, the reset of ongoing

oculomotor processes after peripheral cues (first assumption) has been suggested to be mediated by a direct pathway from the retina to the visual neurons of the SC (Hafed et al., 2015). For endogenous attention, however, this reset is unlikely to be driven by the direct bottom-up processing of the cue stimulus, because the SC lacks the properties to encode the meaning of (symbolic) endogenous cues. Thus, processing endogenous cues crucially depends on cortical processing including frontal, parietal, and higher visual areas (see also Engbert, 2006). Second, ongoing fluctuations in behavioral performance are more common for exogenous attention but not for endogenous attention. Instead, after endogenous cues, behavioral benefits at the to-be-attended location are stable over a period of time (Müller & Rabbit, 1989), despite oscillatory MS biases in the late cue-target interval (see Study 1 and 3). This latter finding challenges an important prediction in the account by Hafed and colleagues, namely that MS orientation and perceptual effects are tightly coupled.

***Microsaccades and attention: Interim Conclusion.*** (Micro)saccades have repeatedly been linked to movement-related changes in perception (Chen et al., 2015; Deubel & Schneider, 1996; Hafed, 2013; Hafed et al., 2011; Kowler et al., 1995; Tian et al., 2016; Yuval-Greenberg et al., 2014), but strong evidence showing that classical effects of spatial cueing are caused by peri-microsaccadic changes in visual processing has yet to be found. Nonetheless, it is crucial that future research clarifies how strongly perceptual changes related to MSs – including not only periods of enhanced but also of suppressed visual processing (recently reviewed in Hafed et al., 2015) – contribute to effects of spatial cueing. We suggest that using

stabilized retinal images during spatial cueing is an excellent tool for unraveling the microsaccade-attention link masked by basic oculomotor demands and may even shed new light on the causal link between MSs and covert attention. For example, it would be interesting to see whether altering biases in MS orientation by stabilizing the retinal image (Tian et al., 2016) leads to similar changes in perpetual performance.

In the light of the present and previous findings, we suggest that MSs do not reflect a single process during the spatial cueing of attention, but different processes that crucially depend on the post-cue time interval (see also Kliegl et al., 2009; Laubrock et al., 2010): After a lateralized endogenous cues, 'rebound' MSs mainly reflect the visual selection of stimuli based on their location and features. This is a noteworthy finding as location- and feature-based visual selection are commonly investigated in the Posner spatial cueing task and the visual search task, respectively. However, we show that both attentional selection mechanisms were triggered in a spatial cueing task with a lateralized endogenous cue and jointly modulated 'rebound' MSs. A systematic movement biases toward a stimulus (the relevant cue or the to-be-attended location) may then improve perceptual processing at that stimulus location. In contrast, MSs that occur later in the cue-target interval may contribute to basic oculomotor needs (e.g., Tian et al., 2016) or to sustained attention (see also *4.1.3 Microsaccade-related visual potentials and covert attention*).

In sum, recent computational models on MS generation and task-related dynamics provide a solid basis for integrating the present results (e.g., Engbert, 2012), but the neural underpinnings of these results need to be further explored. Nonetheless, this

thesis provides evidence that MSs may be seen as a flexible oculomotor tool whose use is determined by and also serves the current task demands.

### 4.1.3 Microsaccade-related visual potentials and covert attention

Despite the omnipresence of MSs in most tasks of cognitive neuroscience, their neural consequences are rarely measured. In fact, MSs were discovered over 100 years ago (Dodge, 1907; reviewed in Wade & Tatler, 2005) and intensively studied in two waves, with the first wave lasting from the 50s to 80s of the 20$^{th}$ century and a second wave that started in the early 21$^{st}$ century. There is now growing evidence that MSs contribute not only to perceptual and oculomotor processes during fixation but also to higher cognitive processes (e.g., reviewed in Rolfs, 2009). Nonetheless, only three early and one more recent study combined EEG and eye tracking to systematically investigate the consequences of microsaccadic retinal image motion (Armington & Bloom, 1974; Armington et al., 1967; Dimigen et al., 2009; Gaarder et al., 1964). In these studies, MSs are followed by synchronized visual activity similar to activity observed after larger saccadic eye movements (e.g., Thickbroom, Knezevic, Carroll, & Mastaglia, 1991), comprising an early positive deflection (i.e., the P1 or also called 'lambda response'; see Evans, 1953) often followed by a negative deflection (i.e., the N1). In Study 2 and 3 we replicated this signature of the mSRP.

Given the neglect of MSs in cognitive neuroscience, even 50 years after the pioneering study by Gaarder and colleagues, we are just beginning to get a deeper understanding of the functional coupling of MSs with electrophysiological correlates of cognitive processes. In Study 3 we show that the visual components

of the mSRP reveal the focus of attention consistent with the idea of an early locus of attentional selection (recently reviewed in Eimer, 2014). In addition, this potential was affected by MS orientation. Both effects are discussed in the following.

***Attentional gain-modulations of the mSRP.*** Apart from the modulations we observed for MS orientation in all three studies, a different light was cast on the microsaccade-attention link when we analyzed the visual brain potential after MSs. Specifically, in Study 1 and 2, MS orientation was strongly correlated with the feature-based selection of the lateralized cue and weakly correlated with the location-based selection of the to-be-attended hemifield. Both correlations were present during the rebound interval in the MS rate, that is, the interval when the selection of the relevant cue stimulus and the endogenous attention shift likely took place (Kinchla, 1992; Van Velzen & Eimer, 2003). In contrast, in Study 3, the visual components of the mSRP were enhanced for the to-be-attended hemifield throughout the cue-target interval. Importantly, this effect of location-based selection built up during the rebound interval, likely reflecting the cue-triggered covert attention shift. After this initial build-up, stronger visual potentials for the to-be-attended hemifield were observed until the target stimulus appeared. This latter effect corresponds to the finding that attention can be sustainably deployed (Posner, 1980). Thus, attention effects observed for both measures, MS orientation and the mSRP, clearly differed with respect to their temporal aspects and the underlying selection mechanism (location- vs. feature-based selection).

The claim that the enhancement of the mSRP with covert attention resembles the location-based selection of the to-be-attended hemifield is supported by several findings: Both visual components of the mSRP, the P1 and N1, revealed a consistent enhancement spatially selective for the to-be-attended hemifield and these effects equaled attention-related modulations of traditional visually-evoked potentials (Hillyard & Anllo-Vento, 1998; Van Voorhis & Hillyard, 1977). Moreover, effects on the mSRP followed the temporal dynamics of endogenous attention (Kinchla, 1992; Müller & Rabbitt, 1989) and were independent of effects associated with the orientation of MSs. Thus, these results suggest that during spatial cueing of attention, MS-related visual potentials do not merely reflect the bottom-up processing of the fixated visual pattern (Armington et al., 1967; Gaarder et al., 1964). In addition, these potentials inform about the top-down modulation of the visual cortex in a similar fashion to the visually-evoked potential observed after a stimulus. Modulations of early visual components by attention – for example, of the P1 which starts around 80 ms post-stimulus and is likely generated in the early extrastriate cortices (Di Russo, Martinez, & Hillyard, 2003; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002) – have been interpreted as the consequence of a mechanism controlling the gain of sensory evoked potentials. This mechanism selectively amplifies the activity of visual neurons with receptive fields for the to-be-attended location. Consequently, all stimuli presented at the to-be-attended location show enhanced amplitudes of their visual response regardless of their features or relevance to the task (Eason, 1981; Harter & Aine, 1984; e.g., reviewed in Hillyard et al., 1998).

An open question remains as to whether visual potentials from MSs contribute to covert attention, especially when the focus of covert attention is maintained over an extended period of time. As sustained covert attention requires to maintain strict fixation, microsaccadic gaze shifts benefit the task by a very basic mechanism, namely retinal image motion. In fact, moving stimuli across retinal receptor cells and generating visual transients is one of the core functions of MSs which serves to prevent visual fading of foveal and peripheral stimuli (Ditchburn, 1980; Engbert & Mergenthaler, 2006; Martinez-Conde et al., 2006; McCamy et al., 2012; but see Poletti & Rucci, 2016).

However, this MS-related refreshing of visual representations is not uniquely related to covert attention, but is also present in other fixation conditions. More specifically, it has repeatedly been shown that visual transients from MSs are likely used for subsequent perceptual judgements in various experimental settings (e.g., Deubel & Elsner, 1986; Martinez-Conde et al., 2006; Troncoso, Macknik, Otero-Millan, & Martinez-Conde, 2008). To maintain covert attention at a to-be-attended location, it may be important to have a stable representation of that location; a process likely guided by sustained top-down signals from frontoparietal areas to the extrastriate cortex (Corbetta & Shulman, 2002; Sarter et al., 2001). One benefit of MSs could be that their visual transients provide information about the current state of this top-down modulation depending on how strongly the MS-related percept is biased toward the to-be-attended location. Importantly, attention does not only enhance visually-evoked potentials but also the way stimuli are perceived. By increasing contrast sensitivity or spatial resolution, an attended stimulus, for

example, the placeholder for the to-be-attended location, appears more intense than an unattended stimulus, for example, the opposite placeholder (e.g., Carrasco, Ling, & Read, 2004; Störmer, McDonald, & Hillyard, 2009; e.g., reviewed in Carrasco, 2011). Thus, although participants may not be aware of executing MSs, they may use the visual transient after MSs to judge if their attention is focused according to the demands of the task. For example, if the MS-related percept is unbiased or even biased toward the not-to-be-attended hemifield, (further) top-down modulation might be initiated.

***Microsaccade orientation and the mSRP.*** In addition to the attention-related enhancement effect, the mSRP was lateralized with respect to MS orientation: The visual components exhibited stronger responses at recording sites ipsilateral to the hemifield the MS moved toward. This finding was independent of the attention effect, for example, it was observed also during the fixation interval. We speculate that this orientation-related enhancement of the mSRP could reflect the bottom-up processing of the stimulus configuration. Since MSs move stationary stimuli across the retina, the foveal stimulation (e.g., the arrow cue) might have been systematically displaced into one hemifield (see also Meyberg, 2011). In line with that, presenting visual stimuli in only one hemifield has been shown to evoke lateralized visual potentials (Chiappa, 1989).

However, this hypothesis was challenged in a follow-up study from our lab in which the modulation of mSRPs by MS orientation and visual properties of the fixated pattern was further explored in a simple fixation task with different visual conditions (i.e., displays with distinct foveal and peripheral stimuli, a uniform grey

background, and in the dark). In brief, the mSRP was modulated by MS orientation regardless of the visual condition, with this pattern being more consistent in the time range of the N1 rather than the P1 component. This results suggests that the orientation-related enhancement of the mSRP instead resembles a non-visual, corollary signal. In fact, corollary signals have not only been observed in the SC or the frontal eye fields as mentioned above (e.g., Hafed & Krauzlis, 2010), but also along the visual pathway (Hass & Horwitz, 2011; Kagan, Gur, & Snodderly, 2008; Martinez-Conde et al., 2000; Meirovithz, Ayzenshtat, Werner-Reiss, Shamir, & Slovin, 2012). For example, in non-human primates, these signals are often reported as a decrease in neural activity (reviewed in Martinez-Conde et al., 2013).

So far, it is an open question whether MSs are accompanied by EEG-recordable corollary signals, but studies on the visual potentials after saccades provide some evidence for these signals (Kazai & Yagi, 2003; Marton & Szirtes, 1982; Skrandies & Laschke, 1997). For example, in the study by Skrandies and Laschke (1997) participants executed horizontal saccades of 15° in a condition without visual stimulation and in the dark. As a result, a P1-like potential was observed which showed a similar lateralization by the orientation of the saccade as in our study (especially in our condition with a tiny fixation point in otherwise complete darkness). Further, the non-visual contributions to the mSRP were of a magnitude smaller than the visually-evoked components; a finding consistent with previous studies on non-human primates (Martinez-Conde et al., 2013). Thus, a modulation of visual transients that relates to the properties of a MS (and saccade) may help the visual system to distinguish active visual stimulation by eye movements from

passive external stimulation and contribute to visual stability during fixational gaze shifts (see also Wurtz, 2008).

A clear limitation of our follow-up study is that a central fixation point was used in all visual conditions. Although this stimulus was very small and dimly lighted, it could still be systematically shifted within one hemifield, consistent with our initial hypothesis. Moreover, in the condition most appropriate to test for non-visual effects, that is, in the dark, we observed pronounced alpha ringing after MSs (see also Dimigen et al., 2009), which complicates the interpretation of the EEG data. Thus, the hypothesis that the orientation-related enhancement of the mSRP resembles a corollary signal needs to be tested in future studies using, for example, a homogenous full-field stimulation without a fixation point.

To summarize, during covert attention MSs not only refresh the visual representation of the fixated display once or twice per second, but also provide the cognitive system with an enhanced representation of the to-be-attended hemifield. In future research it should be tested if this altered representation contributes to visual attention or constitutes a side effect of MSs that mainly serve to keep fixation and to prevent visual fading during prolonged fixation. A further goal should be to examine more closely the modulation of the mSRP by the bottom-up properties of the fixated stimulus pattern, as well as to investigate whether and how strongly non-visual signals contribute to the mSRP. Nonetheless, we show that the mSRP provides a fine-grained measure of how the location-based selection of the to-be-attended hemifield evolves after an attention-directing cue.

## 4.2 Microsaccades: Challenges and perspectives in EEG research

This thesis combined the recording of eye movements and EEG to investigate functional links between MSs and ERP correlates of attention. However, analogous to their larger counterparts, MSs are associated with ocular artifacts (e.g., Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008). Thus, a second objective of this thesis was to evaluate if attention-related ERP effects are produced as the mere consequence of (1) CR artifacts from MSs or (2) overlapping cortical activity originating from the presentation of stimuli and microsaccadic gaze shifts.

In general, an important obstacle in EEG research is to prevent and/or eliminate ocular artifacts that result from the rotation of the corneoretinal dipole, movements of the eyelids during blinks or vertical eye movements, and the contraction of the extraocular muscles at eye movement onset (Keren, Yuval-Greenberg, & Deouell, 2010). These artifacts are not only picked up by the electrodes of the EOG, but also propagate to EEG electrodes. Thus, to reduce ocular artifacts in EEG studies, strict visual fixation is commonly required during the recording. In addition, EEG data are checked offline for excessive eye movements and blinks, for example, by visually inspecting the data or using fixed EOG thresholds (Luck, 2014).

***Microsaccade-related spike potential.*** As shown in Study 2, these conventional procedures for saccade detection may be effective in eliminating artifacts from larger saccades but fail to detect MSs, which are associated with similar ocular artifacts as saccades, albeit of smaller amplitude (e.g., Dimigen et al., 2009; Keren

et al., 2010; Plöchl, Ossandón, & König, 2012). In fact, the consequences of MS-related artifacts in EEG and MEG recordings have been heavily debated recently (e.g., Carl, Acik, König, Engel, & Hipp, 2012; Craddock, Martinovic, & Muller, 2016; Dimigen et al., 2009; Hassler, Friese, Martens, Trujillo-Barreto, & Gruber, 2013; Jerbi et al., 2009; Keren et al., 2010; Plöchl et al., 2012; Yuval-Greenberg et al., 2008). This debate mainly focused on a myogenetic artifact which is characterized by a broad spectral profile overlapping the classical gamma-band in EEG research (Keren et al., 2010; Yuval-Greenberg et al., 2008). In particular, at movement onset MSs are accompanied by a biphasic spike potential, the SP, that is strongest at EOG electrodes, but is also present at posterior EEG sites with an inverted polarity (e.g., see Study 2 and 3). A similar SP has also been observed for saccades and likely results from the summated electrical discharge of the extraocular muscles (Keren et al., 2010; Thickbroom & Mastaglia, 1986, 1987; but see Kurtzberg & Vaughan, 1982).

Importantly, this MS-related SP has been shown to distort the measurement of the 'induced gamma-band response' over posterior areas; an EEG marker that has been related to the synchronous oscillatory activity across a distributed neuronal network for object representation (e.g., Tallon-Baudry & Bertrand, 1999). These distortions arise, if MSs relate to experimental factors. Given the spectral signature of the SP, stronger artifact-related gamma-responses have been observed in conditions and time intervals in which MSs were more frequent (e.g., Hassler, Trujillo Barreto, & Gruber, 2011; Yuval-Greenberg & Deouell, 2009; Yuval-Greenberg et al., 2008).

***Microsaccade-related corneoretinal artifacts.*** In Study 2, we show that MSs not only affect EEG analyses in the frequency domain, but also the measurement of event-related potentials. In particular, microsaccadic shifts of the gaze evoke a CR artifact whose polarity depends on MS orientation and resembles the CR artifact after larger saccades (Berg & Scherg, 1991). However, with an average distortion less than 3 $\mu$V at the horizontal EOG, the MS-related CR artifact falls well below conventional thresholds for EOG-based saccade detection (e.g., horizontal EOG deflections exceeding ± 20 to 100 $\mu$V; see also Dimigen et al., 2009).

In general, CR artifacts from undetected MSs complicate EEG measurements as they reduce the signal-to-noise ratio by adding noise to the data. More specifically, lateralized ERPs especially at frontal recording sites are prone to systematic contaminations by CR artifacts if MS orientation aligns with experimental factors. In fact, lateralized ERPs are a common observation for sensory processing and attention, but also for motor preparation and other higher-level processes such as language processing (for an overview on lateralized ERPs see Luck, 2014). We do not argue that all of these ERPs result from MS-related CR artifacts, but they could be enhanced or reduced in amplitude depending on the direction and strength of task-related MS biases, the polarity of the lateralized ERP, and the electrode sites at which the ERP emerges.

Consistent with that idea, in Study 2, we observed a contamination of the lateralized ERP that is elicited after an attention-directing cue: EEG deflections in the typical time range of the ADAN followed the bias in MS orientation and not, as commonly thought (e.g., Nobre et al., 2000), the direction of the cued attention shift. When we

corrected this artifact by means of ICA (Jung et al., 2000; Plöchl et al., 2012), the frontal part of the ADAN was eliminated. Importantly, our data do not suggest that ADAN is fully explained by a CR artifact, as we still observed a reliable ADAN at central sites in line with previous findings (e.g., Nobre et al., 2000; Van Velzen et al., 2006; Yamaguchi et al., 1994). Nonetheless, the contamination of frontal ADAN by CR artifacts suggests that previous studies need to be re-evaluated carefully, since previous ERP analyses often focused on frontal ADAN (e.g., Green, Teder-Salejarvi, & McDonald, 2005; Seiss, Driver, & Eimer, 2009; Seiss et al., 2007).

***Overlapping brain activity related to microsaccades and stimulus events.*** So far, the line of reasoning focused on how MS-related ocular artifacts contaminate EEG markers. However, MSs are also followed by brain electrical (visual) responses (see Study 2 and 3) that can overlap with the ERP of interest. In fact, it has been shown that these responses can alter the waveform and topographies of late ERPs. In a study by Dimigen et al. (2009), the well-known P300 measured at central sites – that is, a positive deflection likely indexing the contextual updating of working memory (e.g., Donchin & Coles, 1988) – was reduced in trials with a MS during the rebound interval, while activity at occipital sites was increased. Such a pattern would be expected if the P1 component of the mSRP, which shows a positive deflection at occipital sites and negative deflection at central sites, adds to the stimulus-evoked response in that time range.

Such an overlap in brain activity can also go in the other direction. In particular, ERPs may add to MS-related EEG effects. Thus, in Study 3 we investigated whether

the lateralized attention effects of the visual components of the mSRP result from the lateralized cue-ERP that is recorded at similar sites in an overlapping time frame. To this end, we subtracted the cue-ERP from the single trial EEG response of each subjects. As a result, we found no contamination of attention effects of the mSRP, suggesting that these effects are directly related to an attentional gain-control mechanism (see also *4.1.3 Microsaccade-related visual potentials and covert attention*).

***Concluding remarks.*** There is mounting evidence that involuntary MSs pose challenges in cognitive neuroscience that have long been neglected. In principle, each task that requires fixation over a prolonged period of time will be accompanied by MSs and their scalp recordable consequences. For example, Dimigen et al. (2009) found that in a classical oddball task, MSs occurred in up to 86% of trials. However, on the positive side of the controversial debate about MS-related gamma artifacts (e.g., Melloni, Schwiedrzik, Wibral, Rodriguez, & Singer, 2009; Yuval-Greenberg, Keren, Tomer, Nelken, & Deouell, 2009; Yuval-Greenberg et al., 2008) it is to note that this finding has not only raised awareness about the inevitable occurrence of fixational eye movements, but promoted the development of promising methods to account for saccade-related artifacts. Most of these methods perform blind source separation by means of ICA (Jung et al., 2000) and are effective in eliminating and attenuating the MS-related CR artifact and SP, respectively (Craddock et al., 2016; Hassler et al., 2011; Keren et al., 2010; Plöchl et al., 2012). As a simple remedy, some studies selected and resorted trials with respect to MS dynamics and explored MS-related changes in EEG markers (e.g.,

Dimigen et al., 2009; Yuval-Greenberg et al., 2008). Finally, a method is now available to detect MSs via the EOG which can be used to explore the dynamics in MS rate and, thus, also potential contaminations of the gamma-response (Keren et al., 2010). However, this latter method does not provide precise information about MS orientation and amplitude and is therefore, for example, less helpful in unraveling systematic CR artifacts. Consequently, in-depth analyses of MS dynamics still necessitate high-precision eye tracking techniques (Poletti & Rucci, 2016).

Despite the potential threads of saccadic eye movements for scalp-recordable EEG activity, there is a growing interest in the combined recording of eye movements and EEG. This interest stems from the desire to increase the ecological validity of experimental set-ups by relaxing strict fixation requirements and/or allowing the execution of saccades, for example, during reading or free viewing of scenes (e.g., Dandekar, Ding, Privitera, Carney, & Klein, 2012; Dandekar, Privitera, Carney, & Klein, 2012; Dimigen, Kliegl, & Sommer, 2012; Dimigen, Sommer, Hohlfeld, Jacobs, & Kliegl, 2011; Kaunitz et al., 2014; Kornrumpf, Niefind, Sommer, & Dimigen, 2016; Ossandon et al., 2010). In addition, it also takes into consideration that even simple visual fixation is characterized by rich oculomotor and perceptual processes (e.g., Ditchburn & Ginsborg, 1953).

Thus, the combined recording of EEG and eye movements will not only help to get a better understanding of saccade-related artifacts, but it is also a promising methodological approach to deepen our understanding of vision, attention, and oculomotor control. Future research should continue to address how low-level

influences affect the visual components after MSs (Dimigen et al., 2009; Gaarder et al., 1964), but also whether and how pre-saccadic components associated with MS generation and extra-retinal signals contribute to the mSRP (e.g., Berchicci, Stella, Pitzalis, Spinelli, & Di Russo, 2012; Marton & Szirtes, 1982; Skrandies & Laschke, 1997). A new perspective has been opened up in this thesis by showing that the mSRP reflects also higher-cognitive processes such as attention. So far it is unknown if the mSRP is also characterized by classical late ERP components, for example, the P300 or the N400. Such a signature is indicated by the similarity of the mSRP with brain responses after saccades (e.g., Dimigen et al., 2009) and the recent finding that these latter potentials show similar late ERPs as in a condition with passive stimulation (Dandekar, Ding, et al., 2012; Dimigen, Sommer, et al., 2011; Kaunitz et al., 2014). Another open question is if (micro-)saccades are functionally related to brain oscillatory processes. An interesting candidate in the EEG are alpha oscillations which are observed over posterior areas and closely linked to spatial attention; that is, alpha power shows retinotopical changes with covert attention and is linked to perceptual performance (Thut, Nietzel, Brandt, & Pascual-Leone, 2006; Worden, Foxe, Wang, & Simpson, 2000). Evidence consistent with a microsaccade-alpha coupling comes from an early study showing that the phase of ongoing alpha is linked to MS onset (Gaarder, Koresko, & Kropel, 1966; but see Dimigen, Werkle-Bergner, Meyberg, Kliegl, & Sommer, 2011) and a more recent study that observed pronounced alpha ringing after MSs (Dimigen et al., 2009). However, in a spatial cueing study with an endogenous cue, no correlation between the cue-related bias of ‘rebound’ MSs with the well-known

finding of lateralized alpha power was observed (Wieczorek, 2016; PhD thesis). Thus, these different findings need to be clarified in future research.

## 4.3 Conclusion

This thesis provides evidence that the combined recording of high-resolution eye movements and ERPs advances our knowledge about the coupling between MSs and endogenous attention. While MSs have been overlooked in most studies on covert attention to date, we show that these fixational saccades are inherently linked to the location- and feature-based selection of stimuli and to the ERP correlates of these attentional selection mechanisms. Thus, MSs are integrated into the well-established neural networks in control of endogenous attention and, may therefore comprise overt responses during ‘covert attention’ and ‘covert search’.

# References

Allport, D. A. (1987). Selection for action: Some behavioral and neurophysiological considerations of attention and action. In H. Heuer & A. F. Sanders (Eds.), *Perspectives on Perception and Action* (pp. 395-419). Hillsdale, NJ: Lawrence Erlbaum Associates.

Armington, J. C., & Bloom, M. B. (1974). Relations between the amplitudes of spontaneous saccades and visual responses. *J Opt Soc Am, 64*(9), 1263-1271.

Armington, J. C., Gaarder, K., & Schick, A. M. (1967). Variation of spontaneous ocular and occipital responses with stimulus patterns. *J Opt Soc Am, 57*(12), 1534-15349.

Barlow, H. B. (1952). Eye movements during fixation. *J Physiol, 116*(3), 290-306.

Beck, D. M., & Kastner, S. (2009). Top-down and bottom-up mechanisms in biasing competition in the human brain. *Vision Res, 49*(10), 1154-1165.

Berchicci, M., Stella, A., Pitzalis, S., Spinelli, D., & Di Russo, F. (2012). Spatio-temporal mapping of motor preparation for self-paced saccades. *Biol Psychol, 90*(1), 10-17.

Berg, P., & Scherg, M. (1991). Dipole models of eye movements and blinks. *Electroencephalogr Clin Neurophysiol, 79*(1), 36-44.

Betta, E., & Turatto, M. (2006). Are you ready? I can tell by looking at your microsaccades. *Neuroreport, 17*(10), 1001-1004.

Broadbent, D. E. (1954). The role of auditory localization in attention and memory span. *J Exp Psychol, 47*(3), 191-196.

Carl, C., Acik, A., König, P., Engel, A. K., & Hipp, J. F. (2012). The saccadic spike artifact in MEG. *Neuroimage, 59*(2), 1657-1667.

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nat Neurosci, 7*(3), 308-313.

Castet, E., Jeanjean, S., Montagnini, A., Laugier, D., & Masson, G. S. (2006). Dynamics of attentional deployment during saccadic programming. *J Vis, 6*(3), 196-212.

Chen, C. Y., Ignashchenkova, A., Thier, P., & Hafed, Z. M. (2015). Neuronal Response Gain Enhancement prior to Microsaccades. *Curr Biol, 25*(16), 2065-2074.

Chiappa, K. H. (1989). Pattern-shift visual evoked potentials: methodology *Evoked Potentials in Clinical Medicine* (pp. 37-110).

Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural systems? *P Natl Acad Sci USA, 95*(3), 831-838.

Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat Neurosci, 3*(3), 292-297.

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: From environment to theory of mind. *Neuron, 58*(3), 306-324.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci, 3*(3), 201-215.

Cornsweet, T. N. (1956). Determination of the Stimuli for Involuntary Drifts and Saccadic Eye Movements. *J Opt Soc Am, 46*(11), 987-993.

Craddock, M., Martinovic, J., & Muller, M. M. (2016). Accounting for microsaccadic artifacts in the EEG using independent component analysis and beamforming. *Psychophysiology, 53*(4), 553-565.

Dandekar, S., Ding, J., Privitera, C., Carney, T., & Klein, S. A. (2012). The fixation and saccade p3. *Plos One, 7*(11), e48761.

Dandekar, S., Privitera, C., Carney, T., & Klein, S. A. (2012). Neural saccadic response estimation during natural viewing. *Journal of Neurophysiology, 107*(6), 1776-1790.

Desimone, R., & Duncan, J. (1995). Neural mechanism of selective visual-attention. *Annu Rev Neurosci, 18*, 193-222.

Deubel, H. (2014). Attention and Action. In K. Nobre & S. Kastner (Eds.), *The Oxford Handbook of Attention*. Oxford: Oxford University Press.

Deubel, H., & Elsner, T. (1986). Threshold Perception and Saccadic Eye Movements. *Biol Cybern, 54*(6), 351-358.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Res, 36*(12), 1827-1837.

Di Russo, F., Martinez, A., & Hillyard, S. A. (2003). Source analysis of event-related cortical activity during visuo-spatial attention. *Cereb Cortex, 13*(5), 486-499.

Di Russo, F., Martinez, A., Sereno, M. I., Pitzalis, S., & Hillyard, S. A. (2002). Cortical sources of the early components of the visual evoked potential. *Hum Brain Mapp, 15*(2), 95-111.

Dimigen, O., Kliegl, R., & Sommer, W. (2012). Trans-saccadic parafoveal preview benefits in fluent reading: a study with fixation-related brain potentials. *Neuroimage, 62*(1), 381-393.

Dimigen, O., Sommer, W., Hohlfeld, A., Jacobs, A. M., & Kliegl, R. (2011). Coregistration of eye movements and EEG in natural reading: analyses and review. *J Exp Psychol Gen, 140*(4), 552-572.

Dimigen, O., Valsecchi, M., Sommer, W., & Kliegl, R. (2009). Human microsaccade-related visual brain responses. *J Neurosci, 29*(39), 12321-12331.

Dimigen, O., Werkle-Bergner, M., Meyberg, S., Kliegl, R., & Sommer, W. (2011). *Microsaccades and EEG alpha oscillations - a close relationship?* Paper presented at the Frontiers in Human Neuroscience, Conference Abstract: XI International Conference on Cognitive Neuroscience (ICON XI). doi: 10.3389/conf.fnhum.2011.207.00128.

Ditchburn, R. W. (1980). The function of small saccades. *Vision Res, 20*(3), 271-272.

Ditchburn, R. W., & Ginsborg, B. L. (1953). Involuntary eye movements during fixation. *J Physiol, 119*(1), 1-17.

Dodge, R. (1907). An Experimental Study of Visual Fixation. *Psychol Monographs, 8*(4), 1-95.

Donchin, E., & Coles, M. G. (1988). Is the P300 component a manifestation of context updating. *Behav Brain Sci, 11*(3), 357-427.

Eason, R. G. (1981). Visual evoked potentials correlates of early neural filtering druing selective attention. *B Psychon Soc, 18*(4), 203-206.

Egeth, H. E., & Yantis, S. (1997). Visual attention: Control, representation, and time course. *Annu Rev Psychol, 48*, 269-297.

Eimer, M. (1993). Spatial cueing, sensory gating and selective response preparation: an ERP study on visuo-spatial orienting. *Electroencephalogr Clin Neurophysiol, 88*(5), 408-420.

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalogr Clin Neurophysiol, 99*(3), 225-234.

Eimer, M., Forster, B., Van Velzen, J., & Prabhu, G. (2005). Covert manual response preparation triggers attentional shifts: ERP evidence for the premotor theory of attention. *Neuropsychologia, 43*(6), 957-966.

Eimer, M., & Van Velzen, J. (2002). Crossmodal links in spatial attention are mediated by supramodal control processes: Evidence from event-related potentials. *Psychophysiology, 39*(4), 437-449.

Eimer, M., van Velzen, J., & Driver, J. (2002). Cross-modal interactions between audition, touch, and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *J Cogn Neurosci, 14*(2), 254-271.

Engbert, R. (2006). Microsaccades: a microcosm for research on oculomotor control, attention, and visual perception. In S. Martinez-Conde, S. L. Macknik, L. M. Martinez, J. M. Alonso, & P. U. Tse (Eds.), *Visual Perception, Part 1, Fundamentals of Vision: Low and Mid-Level Processes in Perception* (Vol. 154, pp. 177-192). Amsterdam: Elsevier Science Bv.

Engbert, R. (2012). Computational modeling of collicular integration of perceptual responses and attention in microsaccades. *J Neurosci, 32*(23), 8035-8039.

Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Res, 43*(9), 1035-1045.

Engbert, R., & Kliegl, R. (2004). Microsaccades keep the eyes' balance during fixation. *Psychol Sci, 15*(6), 431-436.

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *P Natl Acad Sci USA, 103*(18), 7192-7197.

Engbert, R., Mergenthaler, K., Sinn, P., & Pikovsky, A. (2011). An integrated model of fixational eye movements and microsaccades. *P Natl Acad Sci USA, 108*(39), E765-E770.

Eriksen, C. W., & James, J. D. S. (1986). Visual attention within and around the field of focal attention: A zoom lens model. *Percept Psychophys, 40*(4), 225-240.

Fecteau, J. H., Bell, A. H., & Munoz, D. P. (2004). Neural correlates of the automatic and goal-driven biases in orienting spatial attention. *J Neurophysiol, 92*(3), 1728-1737.

Fecteau, J. H., & Munoz, D. P. (2006). Salience, relevance, and firing: a priority map for target selection. *Trends Cogn Sci, 10*(8), 382-390.

Gaarder, K., Koresko, R., & Kropel, W. (1966). The physic relation of a component of alpha rhythm to fixation saccadic eye movements. *Electroencephalogr Clin Neurophysiol, 21*(6), 544-551.

Gaarder, K., Krauskopf, J., Graf, V., Kropfl, W., & Armington, J. C. (1964). Averaged Brain Activity Following Saccadic Eye Movement. *Science, 146*(3650), 1481-1483.

Galfano, G., Betta, E., & Turatto, M. (2004). Inhibition of return in microsaccades. *Exp Brain Res, 159*(3), 400-404.

Gherri, E., Driver, J., & Eimer, M. (2008). Eye movement preparation causes spatially-specific modulation of auditory processing: New evidence from event-related brain potentials. *Brain Res, 1224*, 88-101.

Gherri, E., & Eimer, M. (2008). Links between eye movement preparation and the attentional processing of tactile events: An event-related brain potential study. *Clin Neurophysiol, 119*(11), 2587-2597.

Green, J. J., Conder, J. A., & McDonald, J. J. (2008). Lateralized frontal activity elicited by attention-directing visual and auditory cues. *Psychophysiology, 45*(4), 579-587.

Green, J. J., Teder-Salejarvi, W. A., & McDonald, J. J. (2005). Control mechanisms mediating shifts of attention in auditory and visual space: a spatio-temporal ERP analysis. *Exp Brain Res, 166*(3-4), 358-369.

Hafed, Z. M. (2011). Mechanisms for generating and compensating for the smallest possible saccades. *Eur J Neurosci, 33*(11), 2101-2113.

Hafed, Z. M. (2013). Alteration of visual perception prior to microsaccades. *Neuron, 77*(4), 775-786.

Hafed, Z. M., Chen, C. Y., & Tian, X. (2015). Vision, perception, and attention through the lens of microsaccades: mechanisms and implications. *Front Sy Neurosci, 9*, 1-16.

Hafed, Z. M., & Clark, J. J. (2002). Microsaccades as an overt measure of covert attention shifts. *Vision Res, 42*(22), 2533-2545.

Hafed, Z. M., Goffart, L., & Krauzlis, R. J. (2009). A neural mechanism for microsaccade generation in the primate superior colliculus. *Science, 323*(5916), 940-943.

Hafed, Z. M., & Krauzlis, R. J. (2010). Microsaccadic Suppression of Visual Bursts in the Primate Superior Colliculus. *J Neurosci, 30*(28), 9542-9547.

Hafed, Z. M., & Krauzlis, R. J. (2012). Similarity of superior colliculus involvement in microsaccade and saccade generation. *J Neurophysiol, 107*(7), 1904-1916.

Hafed, Z. M., Lovejoy, L. P., & Krauzlis, R. J. (2011). Modulation of microsaccades in monkey during a covert visual attention task. *J Neurosci, 31*(43), 15219-15230.

Hafed, Z. M., Lovejoy, L. P., & Krauzlis, R. J. (2013). Superior colliculus inactivation alters the relationship between covert visual attention and microsaccades. *Eur J Neurosci, 37*(7), 1169-1181.

Harter, M. R., & Aine, C. J. (1984). Brain mechanisms of visual selective attention. In R. Parasuraman & B. R. Davies (Eds.), *Varieties of attention* (pp. 293-321). London: Academic Press.

Harter, M. R., Miller, S. L., Price, N. J., Lalonde, M. E., & Keyes, A. L. (1989). Neural processes involved in directing attention. *J Cogn Neurosci, 1*(3), 223-237.

Hass, C. A., & Horwitz, G. D. (2011). Effects of microsaccades on contrast detection and V1 responses in macaques. *J Vis, 11*(3), 3, 1-17.

Hassler, U., Friese, U., Martens, U., Trujillo-Barreto, N., & Gruber, T. (2013). Repetition priming effects dissociate between miniature eye movements and induced gamma-band responses in the human electroencephalogram. *Eur J Neurosci, 38*(3), 2425-2433.

Hassler, U., Trujillo Barreto, N., & Gruber, T. (2011). Induced gamma band responses in human EEG after the control of miniature saccadic artifacts. *Neuroimage, 57*(4), 1411-1421.

Hermens, F., & Walker, R. (2010). What determines the direction of microsaccades? *J Eye Mov, 3*(4), 1-20.

Herrington, T. M., Masse, N. Y., Hachmeh, K. J., Smith, J. E., Assad, J. A., & Cook, E. P. (2009). The effect of microsaccades on the correlation between neural activity and behavior in middle temporal, ventral intraparietal, and lateral intraparietal areas. *J Neurosci, 29*(18), 5793-5805.

Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *P Natl Acad Sci USA, 95*(3), 781-787.

Hillyard, S. A., Vogel, E. K., & Luck, S. J. (1998). Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence. *Philos Trans R Soc Lond B Biol Sci, 353*(1373), 1257-1270.

Hopf, J. M., Boelmans, K., Schoenfeld, A. M., Heinze, H. J., & Luck, S. J. (2002). How does attention attenuate target–distractor interference in vision?: Evidence from magnetoencephalographic recordings. *Cogn Brain Res, 15*(1), 17-29.

Hopf, J. M., Boelmans, K., Schoenfeld, M. A., Luck, S. J., & Heinze, H. J. (2004). Attention to features precedes attention to locations in visual search: Evidence from electromagnetic brain responses in humans. *J Neurosci, 24*(8), 1822-1832.

Hopf, J. M., & Mangun, G. R. (2000). Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. *Clin Neurophysiol, 111*(7), 1241-1257.

Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nat Neurosci, 3*(3), 284-291.

Horowitz, T. S., Fine, E. M., Fencsik, D. E., Yurgenson, S., & Wolfe, J. M. (2007). Fixational eye movements are not an index of covert attention. *Psychol Sci, 18*(4), 356-363.

Ignashchenkova, A., Dicke, P. W., Haarmeier, T., & Thier, P. (2004). Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention. *Nat Neurosci, 7*(1), 56-64.

Jerbi, K., Freyermuth, S., Dalal, S., Kahane, P., Bertrand, O., Berthoz, A., & Lachaux, J. P. (2009). Saccade related gamma-band activity in intracerebral EEG: dissociating neural from ocular muscle activity. *Brain Topogr, 22*(1), 18-23.

Jongen, E. M. M., Smulders, F. T. Y., & Van Der Heiden, J. S. H. (2007). Lateralized ERP components related to spatial orienting: Discriminating the direction of attention from processing sensory aspects of the cue. *Psychophysiology, 44*(6), 968-986.

Jonides, J. (1981). Voluntary versus automatic control over the mind's eye's movement. *Attention and performance IX, 9*, 187-203.

Jung, T. P., Makeig, S., Westerfield, M., Townsend, J., Courchesne, E., & Sejnowski, T. J. (2000). Removal of eye activity artifacts from visual event-related potentials in normal and clinical subjects. *Clin Neurophysiol, 111*(10), 1745-1758.

Kagan, I., Gur, M., & Snodderly, D. M. (2008). Saccades and drifts differentially modulate neuronal activity in V1: effects of retinal image motion, position, and extraretinal influences. *J Vis, 8*(14), 19, 11-25.

Kaunitz, L. N., Kamienkowski, J. E., Varatharajah, A., Sigman, M., Quiroga, R. Q., & Ison, M. J. (2014). Looking for a face in the crowd: Fixation-related potentials in an eye-movement visual search task. *Neuroimage, 89*, 297-305.

Kazai, K., & Yagi, A. (1999). Integrated effect of stimulation at fixation points on EFRP (eye-fixation related brain potentials). *Int J Psychophysiol, 32*(3), 193-203.

Kazai, K., & Yagi, A. (2003). Comparison between the lambda response of eye-fixation-related potentials and the P100 component of pattern-reversal visual evoked potentials. *Cogn Affect Behav Neurosci, 3*(1), 46-56.

Kennett, S., Van Velzen, J., Eimer, M., & Driver, J. (2007). Disentangling gaze shifts from preparatory ERP effects during spatial attention. *Psychophysiology, 44*(1), 69-78.

Keren, A. S., Yuval-Greenberg, S., & Deouell, L. Y. (2010). Saccadic spike potentials in gamma-band EEG: characterization, detection and suppression. *Neuroimage, 49*(3), 2248-2263.

Kinchla, R. A. (1992). Attention. *Annu Rev Psychol, 43*, 711-742.

Klein, R., & Farrell, M. (1989). Search performance without eye movements. *Percept Psychophys, 46*(5), 476-482.

Kliegl, R., Rolfs, M., Laubrock, J., & Engbert, R. (2009). Microsaccadic modulation of response times in spatial attention tasks. *Psychol Res, 73*(2), 136-146.

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences, 16*(12), 606-617.

Ko, H. K., Poletti, M., & Rucci, M. (2010). Microsaccades precisely relocate gaze in a high visual acuity task. *Nat Neurosci, 13*(12), 1549-1553.

Kornrumpf, B., Niefind, F., Sommer, W., & Dimigen, O. (2016). Neural Correlates of Word Recognition: A Systematic Comparison of Natural Reading and Rapid Serial Visual Presentation. *Journal of Cognitive Neuroscience*.

Kowler, E. (2011). Eye movements: The past 25 years. *Vision Res, 51*(13), 1457-1483.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Res, 35*(13), 1897-1916.

Krauzlis, R. J., Lovejoy, L. P., & Zenon, A. (2013). Superior colliculus and visual spatial attention. *Annu Rev Neurosci, 36*, 165-182.

Kustov, A. A., & Robinson, D. L. (1996). Shared neural control of attentional shifts and eye movements. *Nature, 384*(6604), 74-77.

Laubrock, J., Engbert, R., & Kliegl, R. (2005). Microsaccade dynamics during covert attention. *Vision Res, 45*(6), 721-730.

Laubrock, J., Engbert, R., Rolfs, M., & Kliegl, R. (2007). Microsaccades are an index of covert attention: Commentary on Horowitz, Fine, Fencsik, Yurgenson, and Wolfe (2007). *Psychol Sci, 18*(4), 364-366.

Laubrock, J., Kliegl, R., Rolfs, M., & Engbert, R. (2010). When do microsaccades follow spatial attention? *Atten Percept Psychophys, 72*(3), 683-694.

Leopold, D. A., & Logothetis, N. K. (1998). Microsaccades differentially modulate neural activity in the striate and extrastriate visual cortex. *Exp Brain Res, 123*(3), 341-345.

Luck, S. J. (2014). *An introduction to the event-related potential technique*: MIT press.

Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: evidence from human electrophysiology. *J Exp Psychol Hum Percept Perform, 20*(5), 1000-1014.

Maioli, C., Benaglio, I., Siri, S., Sosta, K., & Cappa, S. (2001). The integration of parallel and serial processing mechanisms in visual search: evidence from eye movement recording. *Eur J Neurosci, 13*(2), 364-372.

Makeig, S., Bell, A. J., Jung, T. P., & Sejnowski, T. J. (1996). Independent component analysis of electroencephalographic data. In D. S. Touretzky, M. C. Mozer, & M.

E. Hasselmo (Eds.), *Advances in neural information processing systems* (pp. 145-151). Cambridge, MA: MIT Press.

Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2000). Microsaccadic eye movements and firing of single cells in the striate cortex of macaque monkeys. *Nat Neurosci, 3*(3), 251-258.

Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2002). The function of bursts of spikes during visual fixation in the awake primate lateral geniculate nucleus and primary visual cortex. *P Natl Acad Sci USA, 99*(21), 13920-13925.

Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2004). The role of fixational eye movements in visual perception. *Nat Rev Neurosci, 5*(3), 229-240.

Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Dyar, T. A. (2006). Microsaccades counteract visual fading during fixation. *Neuron, 49*(2), 297-305.

Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Hubel, D. H. (2009). Microsaccades: a neurophysiological analysis. *Trends Neurosci, 32*(9), 463-475.

Martinez-Conde, S., Otero-Millan, J., & Macknik, S. L. (2013). The impact of microsaccades on vision: towards a unified theory of saccadic function. *Nat Rev Neurosci, 14*(2), 83-96.

Marton, M., & Szirtes, J. (1982). Averaged lambda potential and visual information processing. *Studia Psychologica, 24*(3-4), 165-170.

McCamy, M. B., Macknik, S. L., & Martinez-Conde, S. (2014). Different fixational eye movements mediate the prevention and the reversal of visual fading. *J Physiol, 592*(19), 4381-4394.

McCamy, M. B., Otero-Millan, J., Macknik, S. L., Yang, Y., Troncoso, X. G., Baer, S. M., Crook, S. M., & Martinez-Conde, S. (2012). Microsaccadic Efficacy and Contribution to Foveal and Peripheral Vision. *J Neurosci, 32*(27), 9194-9204.

McPeek, R. M., & Keller, E. L. (2002). Saccade target selection in the superior colliculus during a visual search task. *J Neurophysiol, 88*(4), 2019-2034.

McPeek, R. M., & Keller, E. L. (2004). Deficits in saccade target selection after inactivation of superior colliculus. *Nat Neurosci, 7*(7), 757-763.

Meirovithz, E., Ayzenshtat, I., Werner-Reiss, U., Shamir, I., & Slovin, H. (2012). Spatiotemporal Effects of Microsaccades on Population Activity in the Visual Cortex of Monkeys during Fixation. *Cereb Cortex, 22*(2), 294-307.

Melloni, L., Schwiedrzik, C. M., Wibral, M., Rodriguez, E., & Singer, W. (2009). Response to: Yuval-Greenberg et al., "Transient Induced Gamma-Band Response in EEG as a Manifestation of Miniature Saccades." Neuron 58, 429-441. *Neuron, 62*(1), 8-10.

Mergenthaler, K., & Engbert, R. (2010). Microsaccades are different from saccades in scene perception. *Exp Brain Res, 203*(4), 753-757.

Meyberg, S. (2011). *The microsaccadic lambda response as an attentional probe: A study using simultaneous ERP and eye movement recordings.* Germany.

Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *J Vis, 7*(14), 8, 1-16.

Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature, 421*(6921), 370-373.

Müller, H. J., & Humphreys, G. W. (1991). Luminance-increment detection: Capacity-limited or not? *J Exp Psychol Hum Percept Perform, 17*(1), 107-124.

Müller, H. J., & Rabbitt, P. M. (1989). Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *J Exp Psychol Hum Percept Perform, 15*(2), 315-330.

Munoz, D. P., & Everling, S. (2004). Look away: The anti-saccade task and the voluntary control of eye movement. *Nat Rev Neurosci, 5*(3), 218-228.

Neumann, O. (1987). Beyond capacity: A functional view of attention.

Nobre, A. C., Sebestyen, G. N., & Miniussi, C. (2000). The dynamics of shifting visuospatial attention revealed by event-related potentials. *Neuropsychologia, 38*(7), 964-974.

Nothdurft, H.-C., Pigarev, I. N., & Kastner, S. (2009). Overt and covert visual search in primates: Reaction times and gaze shift strategies. *J Integr Neurosci, 8*(02), 137-174.

Ossandon, J. P., Helo, A. V., Montefusco-Siegmund, R., & Maldonado, P. E. (2010). Superposition Model Predicts EEG Occipital Activity during Free Viewing of Natural Scenes. *J Neurosci, 30*(13), 4787-4795.

Otero-Millan, J., Troncoso, X. G., Macknik, S. L., Serrano-Pedraza, I., & Martinez-Conde, S. (2008). Saccades and microsaccades during visual fixation, exploration, and search: Foundations for a common saccadic generator. *J Vis, 8*(14), 21, 21-18.

Pastukhov, A., & Braun, J. (2010). Rare but precious: microsaccades are highly informative about attentional allocation. *Vision Res, 50*, 1173-1184.

Pastukhov, A., Vonau, V., Stonkute, S., & Braun, J. (2013). Spatial and temporal attention revealed by microsaccades. *Vision Res, 85*, 45-57.

Plöchl, M., Ossandón, J. P., & König, P. (2012). Combining EEG and eye tracking: identification, characterization, and correction of eye movement artifacts in electroencephalographic data. *Front Hum Neurosci, 6*(278), 1-23.

Poletti, M., Listorti, C., & Rucci, M. (2013). Microscopic eye movements compensate for nonhomogeneous vision within the fovea. *Curr Biol, 23*(17), 1691-1695.

Poletti, M., & Rucci, M. (2016). A compact field guide to the study of microsaccades: Challenges and functions. *Vision Res, 118*, 83-97.

Posner, M. I. (1980). Orienting of attention. *Q J Exp Psychol, 32*(1), 3-25.

Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. *Attention Perform, 10*, 531-556.

Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annu Rev Neurosci, 13*, 25-42.

Praamstra, P., Boutsen, L., & Humphreys, G. W. (2005). Frontoparietal control of spatial attention and motor intention in human EEG. *J Neurophysiol, 94*(1), 764-774.

Ratliff, F., & Riggs, L. A. (1950). Involuntary motions of the eye during monocular fixation. *J Exp Psychol, 40*(6), 687-701.

Rizzolatti, G., & Craighero, L. (1998). Spatial attention: Mechanisms and theories. In M. Sabourin, F. Craik, & M. Roberts (Eds.), *Advances in Psychological Science* (Vol. Biological and cognitive aspects, pp. 171-198). East Sussex, England: Psychological Press.

Rizzolatti, G., Riggio, L., Dascola, I., & Umilta, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia, 25*(1A), 31-40.

Rizzolatti, G., Riggio, L., & Sheliga, B. M. (1994). Space and selective attention. In C. Umilta & M. Moscovitch (Eds.), *Attention and Performance XV: Conscious and Nonconscious Information Processing* (Vol. 15, pp. 231-265). Cambridge: M I T Press.

Robinson, D. A. (1972). Eye movements evoked by collicular stimulation in the alert monkey. *Vision Res, 12*(11), 1795-1808.

Rolfs, M. (2009). Microsaccades: small steps on a long way. *Vision Res, 49*(20), 2415-2441.

Rolfs, M., Engbert, R., & Kliegl, R. (2004). Microsaccade orientation supports attentional enhancement opposite a peripheral cue: commentary on Tse, Sheinberg, and Logothetis (2003). *Psychol Sci, 15*(10), 705-707.

Rolfs, M., Engbert, R., & Kliegl, R. (2005). Crossmodal coupling of oculomotor control and spatial attention in vision and audition. *Exp Brain Res, 166*(3-4), 427-439.

Ruff, C. C., Blankenburg, F., Bjoertomt, O., Bestmann, S., Freeman, E., Haynes, J. D., Rees, G., Josephs, O., Deichmann, R., & Driver, J. (2006). Concurrent TMS-fMRI and psychophysics reveal frontal influences on human retinotopic visual cortex. *Curr Biol, 16*(15), 1479-1488.

Samuel, A. G., & Kat, D. (2003). Inhibition of return: A graphical meta-analysis of its time course and an empirical test of its temporal and spatial properties. *Psychon B Rev, 10*(4), 897-906.

Sarter, M., Givens, B., & Bruno, J. P. (2001). The cognitive neuroscience of sustained attention: where top-down meets bottom-up. *Brain Res Rev, 35*(2), 146-160.

Seiss, E., Driver, J., & Eimer, M. (2009). Effects of attentional filtering demands on preparatory ERPs elicited in a spatial cueing task. *Clin Neurophysiol, 120*(6), 1087-1095.

Seiss, E., Gherri, E., Eardley, A. F., & Eimer, M. (2007). Do ERP components triggered during attentional orienting represent supramodal attentional control? *Psychophysiology, 44*(6), 987-990.

Shulman, G. L., Ollinger, J. M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Petersen, S. E., & Corbetta, M. (1999). Areas involved in encoding and applying directional expectations to moving objects. *J Neurosci, 19*(21), 9480-9496.

Skrandies, W., & Laschke, K. (1997). Topography of visually evoked brain activity during eye movements: lambda waves, saccadic suppression, and discrimination performance. *Int J Psychophysiol, 27*, 15-27.

Smith, D. T., & Schenk, T. (2012). The Premotor theory of attention: Time to move on? *Neuropsychologia, 50*(6), 1104-1114.

Snodderly, D. M., Kagan, I., & Gur, M. (2001). Selective activation of visual cortex neurons by fixational eye movements: implications for neural coding. *Vis Neurosci, 18*(2), 259-277.

Störmer, V. S., McDonald, J. J., & Hillyard, S. A. (2009). Cross-modal cueing of attention alters appearance and early cortical processing of visual stimuli. *P Natl Acad Sci USA, 106*(52), 22456-22461.

Tallon-Baudry, C., & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends Cogn Sci, 3*(4), 151-162.

Thickbroom, G. W., Knezevic, W., Carroll, W. M., & Mastaglia, F. L. (1991). Saccade onset and offset lambda waves: relation to pattern movement visually evoked potentials. *Brain Res, 551*(1-2), 150-156.

Thickbroom, G. W., & Mastaglia, F. L. (1986). Presaccadic spike potential. Relation to eye movement direction. *Electroencephalogr Clin Neurophysiol, 64*(3), 211-214.

Thickbroom, G. W., & Mastaglia, F. L. (1987). Presaccadic spike potential: a computer model based upon motor unit recruitment patterns in the extraocular muscles. *Brain Res, 422*(2), 377-380.

Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). alpha-Band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection. *Journal of Neuroscience, 26*(37), 9494-9502.

Tian, X., Yoshida, M., & Hafed, Z. M. (2016). A Microsaccadic Account of Attentional Capture and Inhibition of Return in Posner Cueing. *Front Sy Neurosci, 10*, 1-23.

Treisman, A. M. (1964). Selective attention in man. *Brit Med Bull, 20*(1), 12-16.

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cogn Psychol, 12*(1), 97-136.

Troncoso, X. G., Macknik, S. L., Otero-Millan, J., & Martinez-Conde, S. (2008). Microsaccades drive illusory motion in the Enigma illusion. *P Natl Acad Sci USA, 105*(41), 16033-16038.

Tse, P. U., Sheinberg, D. S., & Logothetis, N. K. (2002). Fixational eye movements are not affected by abrupt onsets that capture attention. *Vision Res, 42*(13), 1663-1669.

Tse, P. U., Sheinberg, D. S., & Logothetis, N. K. (2003). Attentional enhancement opposite a peripheral flash revealed using change blindness. *Psychol Sci, 14*(2), 91-99.

Tse, P. U., Sheinberg, D. S., & Logothetis, N. K. (2004). The distribution of microsaccade directions need not reveal the location of attention - Reply to Rolfs, Engbert, and Kliegl. *Psychol Sci, 15*(10), 708-710.

Turatto, M., Valsecchi, M., Tame, L., & Betta, E. (2007). Microsaccades distinguish between global and local visual processing. *Neuroreport, 18*(10), 1015-1018.

van der Lubbe, R. H., Neggers, S. F., Verleger, R., & Kenemans, J. L. (2006). Spatiotemporal overlap between brain activation related to saccade preparation and attentional orienting. *Brain Res, 1072*(1), 133-152.

Van Velzen, J., Eardley, A. F., Forster, B., & Eimer, M. (2006). Shifts of attention in the early blind: An ERP study of attentional control processes in the absence of visual spatial information. *Neuropsychologia, 44*(12), 2533-2546.

Van Velzen, J., & Eimer, M. (2003). Early posterior ERP components do not reflect the control of attentional shifts toward expected peripheral events. *Psychophysiology, 40*(5), 827-831.

Van Voorhis, S., & Hillyard, S. A. (1977). Visual evoked potentials and selective attention to points in space. *Percept Psychophys, 22*(1), 54-62.

Wade, N. J., & Tatler, B. W. (2005). *The moving tablet of the eye*. Oxford: Oxford University Press.

Wieczorek, K. (2016). *Investigating the relationship between microsaccades and oscillations in the human visual cortex: PhD Thesis.*

Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific-band electroencephalography increases over occipital cortex. *J Neurosci, 20*(RC63), 1-6.

Yamaguchi, S., Tsuchiya, H., & Kobayashi, S. (1994). Electroencephalographic activity associated with shifts of visuospatial attention. *Brain, 117*, 553-562.

Yokoyama, T., Noguchi, Y., & Kita, S. (2012). Attentional shifts by gaze direction in voluntary orienting: evidence from a microsaccade study. *Exp Brain Res, 223*(2), 291-300.

Yuval-Greenberg, S., & Deouell, L. Y. (2009). The Broadband-Transient Induced Gamma-Band Response in Scalp EEG Reflects the Execution of Saccades. *Brain Topogr, 22*(1), 3-6.

Yuval-Greenberg, S., Keren, A. S., Tomer, O., Nelken, I., & Deouell, L. Y. (2009). Response to Letter: Melloni et al., "Transient Induced Gamma-Band Response in EEG as a Manifestation of Miniature Saccades." Neuron 58, 429-441. *Neuron, 62*(1), 10-12.

Yuval-Greenberg, S., Merriam, E. P., & Heeger, D. J. (2014). Spontaneous microsaccades reflect shifts in covert attention. *J Neurosci, 34*(41), 13693-13700.

Yuval-Greenberg, S., Tomer, O., Keren, A. S., Nelken, I., & Deouell, L. Y. (2008). Transient induced gamma-band response in EEG as a manifestation of miniature saccades. *Neuron, 58*(3), 429-441.

Zelinsky, G. J., & Sheinberg, D. L. (1997). Eye movements during parallel-serial visual search. *J Exp Psychol Hum Percept Perform, 23*(1), 244-262.

Zuber, B. L., & Stark, L. (1965). Microsaccades and velocity-amplitude relationship for saccadic eye movements. *Science, 150*(3702), 1459-1460.